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Flight and Dispersal of the Mosquito *Culex tarsalis* Coquillett in the Sacramento Valley of California

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The flight habits of the mosquito *Culex tarsalis*, a vector of viral encephalitis, were studied in the rice-growing area of Yolo County in the lower Sacramento Valley from 1959 through 1963. Females were captured in dry ice traps every night the traps were set and in all types of terrain. Apparently there are no real barriers to mosquito dispersal in the valley and the surrounding foothills.

The major flight of this mosquito occurs within two hours after sunset and most of the females appear to fly within 50 feet of the ground. When they emerge from their daytime resting places they tend to head into the wind, and at low wind velocities they disperse in all directions. Winds of 3 or 4 miles per hour catch the mosquitoes sooner or later and carry them downwind. Winds of 6 mph and more are apt to inhibit flight. We calculated actual flying speed over a short distance at 4.75 mph.

We have observed this mosquito in flight at temperatures between 55° and 92° F, but usually its activity is reduced below 65° and increased between 65° and 75°. Flight activity is governed by light intensity in relation to temperature and is affected also by wind and other factors.

We marked and released approximately 253,000 females of this species and recaptured 585 of them (0.23 per cent). In these experiments we recorded natural dispersal as far as 5 miles downwind on the night of release and 15.75 miles downwind two nights later. As the chances against recapturing any particular specimen are enormous and increase with distance, it seems certain that this mosquito spreads beyond any of the recovery sites. Probably it travels 8 or 10 miles in two evenings, and we believe that it can spread in one generation, with the prevailing SSE winds, at least 20 or 25 miles from its breeding areas.

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S. F. Bailey, D. A. Eliason, and B. L. Hoffmann

Flight and Dispersal of the Mosquito *Culex tarsalis* Coquillett in the Sacramento Valley of California[1, 2]

INTRODUCTION

THE MOSQUITO *Culex tarsalis* Coq. is the principal vector of viral encephalitis in California. In 1958 the late Stanley B. Freeborn, then Chancellor of the University of California at Davis and a member of the board of trustees of the Sacramento-Yolo County Mosquito Abatement District, proposed a study of the flight range of this mosquito, to meet a need of the mosquito-control agencies. The Sacramento-Yolo County Mosquito Abatement District conducted a survey in 1959 (Umberger, 1960). Professors Freeborn and Bohart, of the Department of Entomology, Davis, implemented studies the same year.

The senior author became affiliated with this project in the early summer of 1960 and made every effort to carry out the original plan—to determine how far *C. tarsalis* may fly from the rice fields, its principal breeding habitat in the Sacramento Valley. With such knowledge investigators could determine to what extent this mosquito could reinfest a controlled area and, if infected, could carry the encephalitis virus. Our immediate project was to release and recapture marked females of this species, to determine if they can and do travel as far in a summer as some residents, entomologists, and officials believe. As the work progressed, the research team came to realize that the scope of the project, realistically, should cover all aspects of the flight and dispersal of this mosquito. Specific objectives were to determine (1) the maximum wind velocity against which it could fly and (2) the maximum distance it could travel in one evening with the aid of the wind.

MOSQUITO DISPERSAL

The literature on the dispersal of insects is voluminous, particularly that on the pest species and most particularly on mosquitoes. Clements (1963) covered the general subject thoroughly. Thurman and Husbands (1951) captured *Aedes nigromaculis* (Ludlow), an irrigated-pasture mosquito, in California 1⅞ miles from the release point and summarized flight records for mosquitoes in other countries—giving a maximum distance of 7.3 miles. Smith, Geib, and Isaak (1956) demonstrated that marked individuals of this species mi-

[1] Submitted for publication August 24, 1964.

[2] Research conducted under Grant No. E-2831, National Institutes of Health, Tropical Medicine and Parasitology Study Section.

grated in large numbers with wind currents as far as 28 miles in the lower San Joaquin Valley of California.

The salt-marsh mosquitoes are strong fliers. Curry (1939) captured *Ae. sollicitans* (Walker) 110 miles at sea off the coast of North Carolina. Aarons *et al.* (1951) marked an estimated 2 million specimens of *Ae. dorsalis* (Meigen) and *Ae. squamiger* (Coquillett) and recovered specimens as far as 38 miles downwind in the San Francisco Bay area. Provost (1957) recovered marked specimens of *Ae. taeniorhynchus* (Wiedemann) as far as 25 miles downwind. Elmore and Schoof (1963) demonstrated the migration of this species for 18 miles on the Atlantic coast.

There is a general belief that anophelines do not fly so far as other mosquitoes. Eyles (1944) reviewed this phase of the subject and wrote: "Investigators have found widely varying results when studying the influence of wind on anopheline flight, indicating a possible difference among species." Bates (1949) made the following observation concerning the flight range of anophelines: "Whether they make long direct flights or disperse through short flights with frequent stops—not much is known. Almost certainly species would vary greatly in this respect, and the same species may show different behavior in different physiological states." Both Kirkpatrick (1925) and Garrett-Jones (1950) captured *Anopheles pharoensis* Theobald in the Egyptian desert many miles from the nearest breeding site—Kirkpatrick at distances of 35 to 45 miles, Garrett-Jones at 18 to 28 miles. Both of these authors believed that the prevailing winds had carried the mosquitoes and that the distances of dispersal might be even greater than their records showed. Garrett-Jones wondered ". . . is it not possible that one or more species has in the past reached such a place as the Siwa Oasis—on a wind which could travel 200 miles across the desert in one night?" Eyles, Sabrosky, and Russell (1945) recovered marked specimens of *A. quadrimaculatus* Say at 3.63 miles.

Much less is known of the movements of *Culex* species. Clarke (1943) recaptured marked specimens of *C. pipiens* Linnaeus at 14 miles in Illinois but made no special mention of the effect of wind on these flights. Reeves, Brookman, and Hammon (1948) recaptured marked specimens of *C. tarsalis* quartering upwind 2.5 miles from the release point in Kern County, California, but they did not publish any data on wind velocities. Their mosquitoes were fed rhodamine-B in sugar solution and held in cans from three to seven days before release, and these conditions undoubtedly affected their flight range. A more recent report (Dow, Reeves, and Bellamy, 1965) extends the recapture distance to a maximum of 9.6 miles.

Horsfall (1942) captured *Psorophora confinnis* (Lynch-Arribalzaga) in Arkansas 9 miles from its breeding site in rice.

THE STUDY AREA

The major part of the present study was conducted on the west side of the Sacramento River in the vicinity of Knights Landing (population 3,042) in Yolo County, in the lower part of the Sacramento Valley. Portions of Sutter and Colusa counties along the river and adjacent to Yolo County— and largely without mosquito control—were included in the study.

On the average about 150,000 acres in four adjoining counties and another 100,000 acres in four other counties are planted to rice every year. The flooded land creates a major mosquito problem. Two species—*Culex tarsalis* and *Anopheles freeborni* Aitken—are disease vectors as well as major pests to man and his livestock over hundreds of square miles.

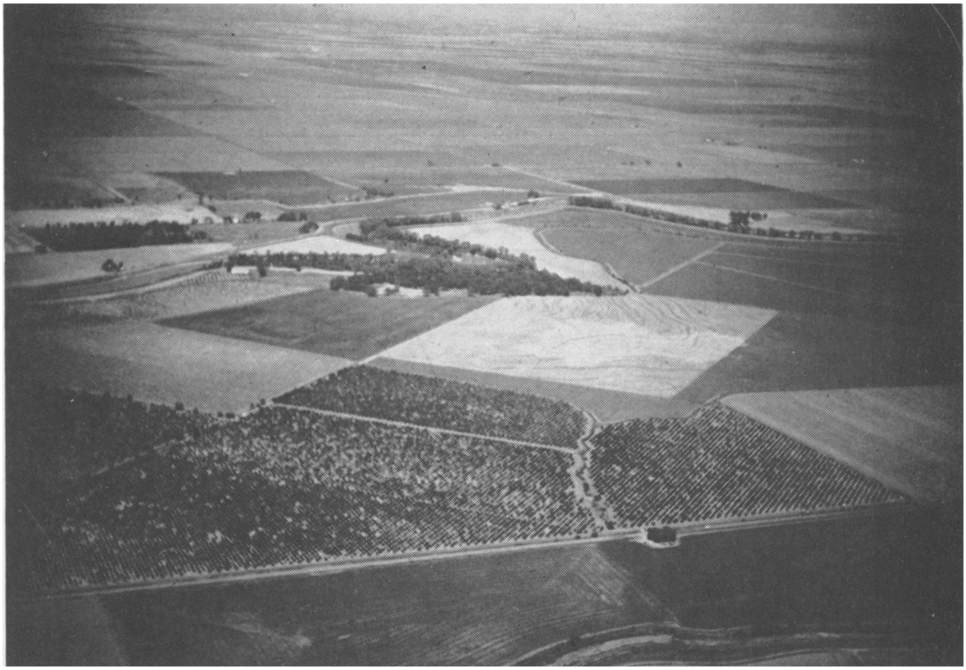

Fig. 1. Agricultural area northwest of Knights Landing, California, showing topography and the diversity of crops. (Aerial photo by C. G. Moore.)

The towns and residential communities in the area are small, usually separated by 10 to 15 miles of agricultural land. The largest city is Woodland, with a population of 16,250. Diverse crops—including alfalfa, beans, rice, safflower, sugar beets, tomatoes, and a few tree crops—are grown in this part of the valley (fig. 1) and nearly all are irrigated. The rice fields are flooded in early May and drained about the middle of September. On some crops the irrigating season extends into October.

Weather Station

In summer the daily temperatures in this part of the Sacramento Valley fluctuate widely—often from 65° F at 5:00 AM[3] to 100° F at 4:00 PM. We maintained a Foxboro[4] weather station (fig. 2), operated from a 6-volt automobile battery, in the rice area three quarters of a mile east of Knights Landing during four summer seasons. This field equipment gave continuous, permanent records of temperature, wind velocity, and wind direction. The highest temperature recorded during the experiments was 108° F on June 15, 1961, and the lowest was 52° F on September 13, 1961.

At this latitude (38° 30′ north) the daylength on June 20 is 14 hours and 52 minutes; on July 20, 14 hours and 30 minutes; on August 20, 13 hours and 30 minutes; and on September 20, 12 hours and 15 minutes.

Winds

A cooling wind from the ocean usually blows up the Sacramento River in the late afternoon or early evening, fans out in the lower valley, and is dissipated about 50 miles north of the Davis-Sacramento area. Normally it diminishes after 10 PM. As the wind follows

[3] Pacific Daylight Saving Time is used throughout this report.

[4] California Spot Climate Station, The Foxboro Company, Foxboro, Massachusetts.

the river, its direction in the experimental area is quite consistently from the south or the southeast, especially at velocities above 3 miles per hour (mph). The direction of the slight summer breezes is more changeable.

When the ocean wind blows steadily for two or three days it cools the entire valley, but such periods are followed by rising temperatures. We encountered also an occasional east wind in the northeastern part of Yolo County. South of Woodland the wind was nearly always directly from the south, but west of Woodland it was frequently from the southwest. On a very few evenings it blew briefly from all directions, especially in areas near pronounced bends of the river.

Strong north winds sweep down the valley at irregular intervals, but no north winds occurred on the nights of our mosquito releases. The following analysis[5] of nighttime winds at Davis is based on official records for 1954 through 1958. It shows how little north wind there is on summer nights. The figures are percentages of the total number of nighttime hours (8:00 PM to 8:00 AM) in July and in August of all five years.

WIND DIRECTION	JULY *per cent*	AUGUST *per cent*
North (NE–NW)	2	1
East (ENE–ESE)	0	0
South (SE–SW)	88	85
West (WSW–WNW)	0	0
Variable	6	7
Calm	4	7

Although wind patterns are probably different in other parts of the Sacramento Valley, we used the official weather charts for Davis to compile a cumulative record of the numbers of hours when winds blew from the north at velocities of 2 mph or higher. The following tabulation covers the 72 nights from June 21 through August 31 each year—the period when *C. tarsalis* is most abundant in the Sacramento Valley.

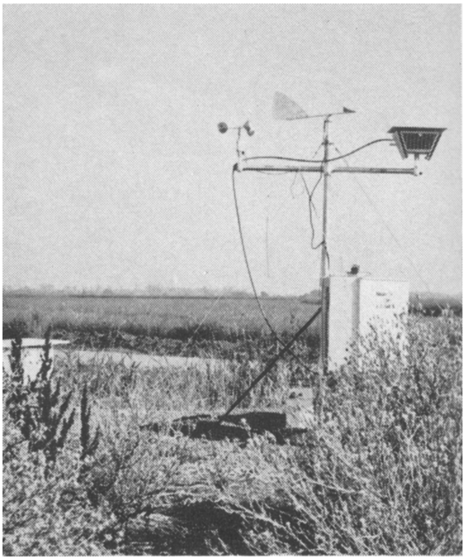

Fig. 2. Field weather station in rice-growing area near Knights Landing, California.

SUMMER	8 PM TO 7 AM *hours*	8 PM TO MIDNIGHT *hours*
1958	7.0	0.5
1959	88.0	4.0
1960	69.5	13.0
1961	47.1	4.0
1962	29.0	0.0
1963	22.3	7.0
Total	262.9	28.5
Average	43.8	4.75

On only four nights in the six summers studied were there north winds of more than 10 mph. Moreover, only 28.5 (10.8 per cent) of the 263 nighttime hours of north wind—an average of 4.75 hours per summer—occurred before midnight, the most significant time for mosquito-flight studies.

[5] Unpublished study by Professor Herbert B. Schultz, Department of Agricultural Engineering, Davis.

EXPERIMENTAL METHODS

The mosquitoes released in 1959 were reared in the laboratory and those released in 1960 were reared in wooden tubs near a rice field in the study area. However, rearing adult mosquitoes for release experiments used up too much of the short summer season, and in 1961 we found that we could trap large numbers of recently emerged, blood-seeking females of *C. tarsalis* in the rice fields or on the bordering levees. Thereafter each experiment involved trapping mosquitoes on one night, marking and releasing them the next evening, and running recovery traps for two or three nights.

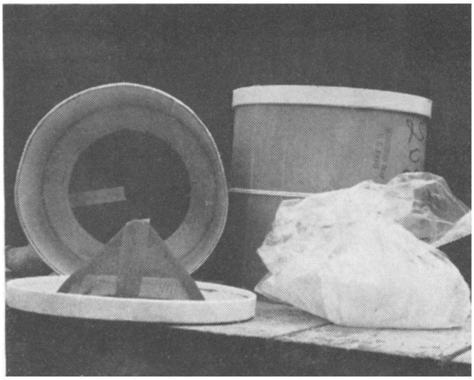

Fig. 3. CO_2 trap made from a 3-gallon ice cream carton with an inverted cone of plastic screening at each end. Bait is a cake of dry ice. Its wrapping (prefabricated plastic bag) is constricted loosely with a rubber band.

Trapping for Fresh Mosquito Material

Bellamy and Reeves (1952) used and described a dry ice trap for *C. tarsalis* and our group modified the design for this work (Bailey, Eliason, and Iltis, 1962). We used either a 4-gallon metal food can with a copper-screen cone at each end or an expendable cardboard trap (fig. 3) that we made on the same design from a 3-gallon ice cream carton with plastic-screen cones. The cardboard trap is equally effective and much cheaper but does not withstand hard use. The removable covers on the metal cans were held in place by rubber bands (shown in fig. 4).

The bait was a 3- to 4-pound block of dry ice, wrapped in newspaper in 1961, thereafter in a plastic bag constricted loosely with a rubber band. When the dry ice released carbon dioxide (CO_2), the gas pressure inflated the bag and the trapped gas insulated the block of ice from the warm evening air so that the dry ice vaporized rather slowly. This bait is effective for *C. tarsalis* because the CO_2 exhaled by an animal is the signal which attracts the blood-seeking female mosquito, and only blood-seeking females are found in a CO_2 trap (Huffaker and Back, 1943).

These traps caught relatively few females of other mosquito species, for reasons not entirely understood—except that *C. tarsalis* seemed the most able to detect unwarmed CO_2. This species made up 98 per cent of all mosquitoes trapped by CO_2 in the rice study area in July, 1961, and 96 per cent of all individuals identified in the recapture experiments during the five years.

When traps were positioned in the field before sundown a bag of dry ice from an insulated chest was placed in each trap. The ice lasted six hours or longer, depending on the temperature, and this was sufficiently long to catch the major flight of mosquitoes. We measured evaporation time on September 11, 1962. Starting at 5:00 PM, an unwrapped 1-pound block of dry ice in a metal trap evaporated completely in four hours, a 3-pound block in six and a half hours, and a 5-pound block in 11 to 13 hours. The air temperature at the site was 83° F at 5:00 PM, 61° at 9:00 PM, 56° at 11:30 PM, and 50° to 52° at 4:00 to 6:00 AM.

To simulate more closely the breath of a living animal we constructed an apparatus which passed CO_2 from a canister of dry ice into the bottom of a 5-gallon can of hot water and delivered warm, moist CO_2 into a trap. In two experiments (both in oak trees) the mosquitoes definitely preferred this bait when it was placed beside a trap with the usual dry ice bait. In the town of Knights Landing on September 6, 1962, the cold trap captured seven specimens of *C. tarsalis* and the trap with warmed bait captured 48. In a rural area one week later the cold trap captured 157 and the trap with warmed bait captured 772. However, *C. tarsalis* came to cold bait readily when no warmed bait was provided. The total catch of this species in the two adjacent traps for each of these tests was little if any higher than the usual catch in a cold CO_2 trap at a similar site. Besides *C. tarsalis* the trap with warmed bait in the rural location caught 200 specimens of *Anopheles freeborni* and also some *Aedes* mosquitoes. It was not practical to use the warming apparatus on a large scale, especially as our project concerned only *C. tarsalis.*

Holding Cages

When the operator picked up the traps in the morning—before predators could destroy the catch—he plugged the openings in the screen cones with cotton. At Davis, working outside the greenhouse, he replaced the removable lid of the trap with a cloth sleeve and blew into the fixed cone, at the lower end of the trap, inducing most of the mosquitoes to fly up through the sleeve into a holding cage of wire mesh, 18″ × 18″ × 26″. We estimated the number of mosquitoes in each cage by counting those resting on one fourth of each side, as demarcated by string guides (fig. 4, *upper right*).

The greatest number of mosquitoes put into any cage was about 5,000, and nearly all of these were *C. tarsalis.* Of course some individuals of other species were trapped, marked, and released along with the species being studied. When a marked mosquito of another species was recaptured it was identified and recorded.

The holding cages were kept in a greenhouse during the day, covered with wet burlap sacks (greenhouse temperature was about 80° F), and transported to the release site about sunset. In early experiments we caused considerable mortality by transporting mosquitoes in the hottest part of the day.

Marking

Bailey, Eliason, and Iltis (1962) reviewed the subject of marking and recovery techniques. We found that the fluorescent Helecon products[6]—nontoxic zinc sulfide dusts, originally used by Reeves, Brookman, and Hammon (1948)—were the most satisfactory of the marking materials tested. They adhered well and could be distinguished quickly from the naturally occurring fluorescence on some wild mosquitoes. Later we introduced certain innovations, described below, in techniques of applying these dusts, and we used them to mark all mosquitoes released in these experiments, with the following exceptions:

1. In 1960 we tried various methods of marking. In 1961 we fed soluble fluorescent materials to the mosquitoes released in the first five experiments (two fifths of all those marked in 1961), but not all individuals fed equally on the solutions offered. Moreover, those engorged with sugar solution did not behave normally. They were sluggish and flew only short distances. The sugar meal did not prevent their being attracted to the CO_2 traps, because it did not satisfy their need for a blood meal. External dusting in addition to the rhodamine feeding did not seem to harm the mosquitoes (releases of August 2 and 20, 1961). These mosquitoes were easy to recognize and the fluorescence, whether from dusting or from feeding,

[6] Dusts 1757, red; 1953, green; 2200, blue; 2267, gold; and others, from U.S. Radium Corp., Morristown, New Jersey.

Fig. 4. Blowing mosquito catch from metal trap through cloth sleeve up into holding cage.

remained bright for as long as three years in the case of the well-marked specimens when stored dry.

2. Radioisotopes have been used to tag mosquitoes (Thurman and Husbands, 1951; Smith, Geib, and Isaak, 1956; Provost, 1957). We experimented briefly with feeding mosquitoes in the laboratory on P^{32} in sugar solution at 10 microcuries per milliliter. The radioactivity of these mosquitoes showed a normal rate of decay and was not lost after a blood meal; about two thirds of it was passed on to the eggs. On July 24, 1962, we released approximately 2,000 mosquitoes made radioactive by such feeding but recaptured none of them.

3. Metallic bronzing powder—Venus White Gold, 54[7]—was dusted on 2,900 mosquitoes released September 5, 1962; four of these individuals were recaptured on Night 1. We marked 2,600 mosquitoes with Helecon dust, released them from the same location immediately after we had released the bronzed specimens, and recaptured 22 of them on Night 0. We observed in both laboratory and field tests that the coarse bronzing powder was clearly visible but did not adhere to all specimens so well

[7] U.S. Bronze Powder Works, Inc., Flemington, New Jersey.

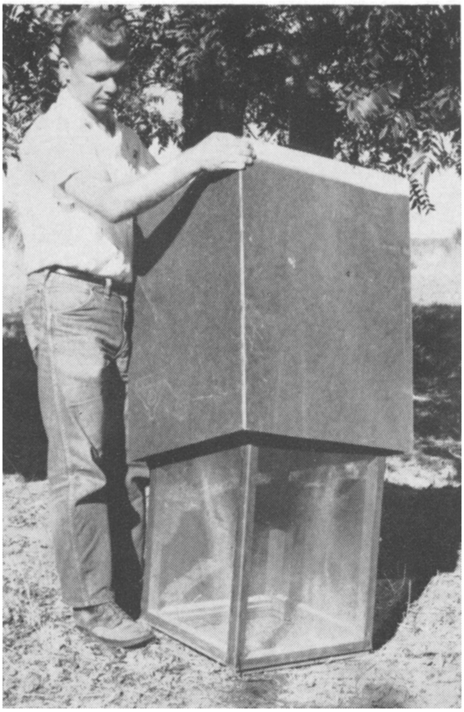

Fig. 5. Holding cage with box-shaped cover that confines the marking powder when it is blown into the cage. Powder is injected into the cage through five half-inch holes in the cover, but only one of the five is clearly visible.

as did the Helecon dust, nor did the bronze powder persist well when the mosquitoes were handled. Rapid scanning with ultraviolet light did not give ready detection of bronzed specimens.

We marked the mosquitoes at the release site while they were still in the holding cages. First we covered each cage, temporarily, with a specially constructed box (fig. 5) or with wrapping paper to confine the dust. We used a large rubber bulb to blow marking powder into the cage through half-inch holes—one in the top of the box or paper cover and one in each of the four sides. The cloud of powder filled the cage and excited the mosquitoes so that they flew around in it until they all received a good coating. Samples from several cages, examined under ultraviolet light, showed that five or six puffs of dust were enough to cover all individuals.

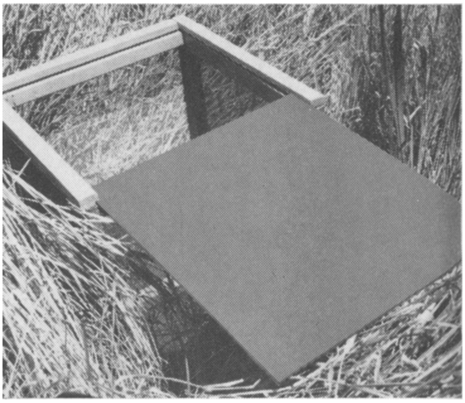

Fig. 6. Holding cage inverted and opened at a release site. Mosquitoes escape when operator removes the sliding floor of the cage.

For each of four successive releases we used a different dust, selected for color contrast and adherence. The distinctive colors identified recaptured mosquitoes from the separate experiments started over a month's time. To avoid possible contamination of the traps or other equipment by the variously colored powders, we transported the dusted cages in a separate vehicle, used only for this purpose. After each dusting we washed all cages and covering boxes thoroughly, and we carried the clean cages containing fresh mosquitoes in a clean truck.

Release

Figure 6 shows a cage inverted and opened to release the catch. We found in 1960 that mosquitoes released in the daytime did not react normally. Thereafter we marked and released the mosquitoes about half an hour after sunset.

We recorded weather conditions five feet above the ground at the site and at the time of every release. As it happened the wind was southerly whenever we started one of the dispersal experiments in the rice fields or their vicinity. At those times it had a range between 0 and 9.1 mph. For wind velocity determinations we averaged three three-minute readings taken at intervals of 15 or 20 minutes with a portable, sensitive anemometer.[8] We took temperature and relative humidity readings with a sling psychrometer and used a compass to check the direction of the wind.

Recapture

For most of the recapture experiments we used the same CO_2-baited traps, placed at the designated locations shortly before sunset. Two men with one vehicle can place a maximum of 50 or 55 traps on a round trip of 50 to 60 miles. Trapping in a complete circle with a radius of 10, 15, or 20 miles around the release point would require many hundreds of traps, but the most our group could handle was 100. Therefore at the greater distances we placed traps only in the downwind quadrant, where there was some probability of recapturing a few specimens.

Analysis of the recaptures in 1961 and 1962 shows that the greatest catch of marked mosquitoes was obtained on the night of release (Night 0) and that those taken on Night 0 plus Night 1 (the first night thereafter) accounted for 91.8 per cent of all the recaptures. Because the marked mosquitoes may continue to disperse nightly and because CO_2 attracts only a blood-seeking female, the odds against recapture increase very greatly from one night to the next, and there appeared to be little point in running traps after Night 2.

Placement of traps for maximum recovery of marked mosquitoes is of great importance. Best results were obtained in traps placed about 5 feet above the ground, fixed to prevent excessive swinging, and oriented individually on a southeast-northwest axis so the prevailing evening breeze would pass through the screened ends. Placing traps closer together than 50 yards did not appear to increase the total catch. Poor catches were obtained from traps placed in dense foliage or near paved areas, or in windy spots such as exposed knolls or levees. The best catches were taken consistently on the lee sides of trees, levees, buildings, or other shelter, and at the margins of wooded areas and streams, particularly at a bend or elbow of a ditch or stream.

When mosquitoes are able to fly into a light wind they may direct their flight to a source of CO_2. When they are carried downwind they seem to catch the CO_2 signal after they have passed the trap and then quarter back upwind to enter the trap.

The recapture traps picked up in the morning contained a considerable amount of moisture. They were left stacked for about two hours in the canopy-covered pickup trucks, where portable electric heaters dried the traps and killed the mosquitoes at the same time. The dry, dead mosquitoes were easily shaken through a funnel into labeled cartons (fig. 7). Each trap catch was later spread on a sheet of black mat construction paper in a darkroom, where an ultraviolet lamp[9] was passed rapidly over the thousands of mosquitoes. The marked specimens were picked out with forceps and saved for the record, but all the mosquitoes were counted and identified. Table 1 gives a sample of the numbers often handled in one day, the variety of species captured, and the variations from trap to trap. The footnote to table 2 names all the species taken in our dispersal experiments.

In 1959, 1960, and early 1961 we tested two other types of traps for recapture. We found CO_2-baited traps the most satisfactory for these experiments, though probably other traps would be better for other work, such as sampling mosquito populations as a guide in control operations. When we used the standard red-box resting unit it took about half a day to chloroform and label the collections from 40 boxes. To sort and count catches from light traps

[8] C. F. Casella & Co., Ltd., London.

[9] Stroblite (Stroblite Co., Inc., 75 West 45th Street, New York 36), with 100-watt spot or flood bulb and a purple-blue filter giving a spectrum of 3,500 to 3,900 Å.

Fig. 7. Transferring dried mosquitoes from trap to carton for later examination.

(New Jersey model, modified) was very laborious because these traps caught many kinds of insects, and moth scales reflected the longer wavelengths of light from the ultraviolet lamp so as to obscure the fluorescent markings on some poorly marked mosquitoes (those with only two or three small dust particles).

Age of Mosquitoes Used in Experiments

We feel that the mosquitoes caught in or near rice fields in CO_2-baited traps and used for our releases were young and of a fairly uniform age—probably two or three days. Most of the many thousands of specimens appeared to be very fresh, with little of the loss of scales that would be expected in older individuals. Moreover, fresh papers in the holding cages were always copiously spattered with bluish meconium spots.

We attempted to determine the ages of mosquitoes in sample collections but found the Detinova (1962) method of dissecting out the ovaries very time-consuming. We examined 343 CO_2-trapped females, some from the rice area and some from a nearby village. As expected, all of the mosquitoes baited by CO_2 had ovaries at Stage I or possibly at early Stage II; none were teneral individuals—recognizable by remnants of the larval muscles. Collections from resting boxes in the village contained older individuals but no teneral females. Those from resting boxes in the rice fields contained teneral and blood-fed individuals as well as specimens with ovarial tracheoles at each of the physiological stages illustrated by Kardos and Bellamy (1961.)

TABLE 1

PORTION OF RECORD FOR ONE NIGHT'S CO_2 TRAP COLLECTION
(Catch of Night 1 following June 19 release at Knights Landing; examined June 21, 1962)

Trap and ground cover	Number of mosquitoes (females only)		
	Culex tarsalis	*Anopheles freeborni*	Other species
1, Rice field	66	0	0
2, Rice field	146	1	0
3, Dry	171	0	3, damaged
4, Dry	162	0	0
5, Dry	12	0	0
6, Dry	12	0	0
7, Dry	288	3	3, *Culex peus* 2, *Aedes* sp.
8, Dry	354	4	1, *Culex erythrothorax* 2, *Aedes* sp.
9, Dry	179	5	1, *Culex erythrothorax* 3, *Aedes* sp.
10, Levee	17	0	0
11–54	7,378	100	261, *Culex peus* 4, *C. pipiens* 2, *Culex* sp. 21, *Aedes* spp. 12, Unidentifiable

NOTES: In the 54 traps there were 9,213 mosquitoes of all species, including a few damaged or otherwise unidentifiable specimens. *Culex tarsalis* made up 95.3 per cent of the total catch. In the rice fields individual traps contained from 21 to 752 mosquitoes of this species; in dry locations (weeds, stubble, safflower), 3 to 354 including one marked specimen (trap No. 7); on levees, 17 to 856; among trees, 51 to 536; in fields of irrigated crops, 43 to 368 including one marked specimen (trap No. 41); and in farmyards, 13 to 442. Twenty-three specimens of *A. freeborni* were found in one trap in a dry location, 20 specimens in one trap on a levee, from 1 to 9 specimens each in 23 traps, and no specimens in 29 of the traps.

We assume that *C. tarsalis* has no migratory stage between emergence and blood-seeking, and Bellamy and Reeves (1952) were of the same opinion. Our only evidence is that the mosquitoes for release experiments were obtained in or near their breeding area and were already craving blood, as indicated by the attraction of the CO_2 bait. Likewise, the recaptured individuals were blood-seeking females. In the early 1962 experiments a few marked specimens were recaptured on Nights 7, 8, and 9. These may have been seeking a second blood meal. Probably their maximum age was 11 or 12 days.

DISPERSAL EXPERIMENTS

In this kind of research the workers can expect to recover fewer than 1 per cent of the marked specimens. Table 2 summarizes the 37 release-recapture experiments carried out from 1959 through 1963. During that time approximately 253,000 marked mosquitoes were released and 585 were recaptured, an overall recovery of 0.23 per cent. The distance of attempted recapture was extended each year by placing traps at greater distances from the release site. The average recovery decreased correspondingly, from 0.89 per cent in 1959 to 0.11 per cent in 1963.

1959 Experiments

In these preliminary experiments we released 561 laboratory-reared mosquitoes of both sexes and recaptured five of them—four males and one female—in light traps 42 feet from the release site (the maximum trapping distance).

1960 Experiments

We made six releases in 1960 and recaptured 26 marked mosquitoes—all in the rice fields, at short distances. The CO_2 traps were operated 15 nights in connection with the recapture experiments, at a maximum distance of 1 mile

TABLE 2
SUMMARY OF RELEASE-RECAPTURE EXPERIMENTS
(Yolo County, California)

Year	Number of experiments	Marked mosquitoes				Additional catch: *C. tarsalis*, unmarked
		Approximate number released	Recaptured			
			Total number	Season's average, as per cent of number released	Maximum recapture distance	
1959	2	561	5	0.89	42 ft.	404
1960	6	3,950	26	0.66	0.43 mi.	10,103
1961	10	40,500	223	0.55	3.0 mi.	105,947
1962	12	140,200	254	0.19	9.3 mi.	299,223
1963	7	67,850	77	0.11	15.75 mi.	59,126
	37	Approx. 253,000	585	Av. 0.23		474,803

NOTE: Approximately 20,000 mosquitoes of other species were captured during these experiments, identified, and counted. The majority of them were *Anopheles freeborni* Aitken. Other local species captured in small numbers were: *A. franciscanus* McCracken, *Aedes melanimon* Dyar, *Ae. nigromaculis* (Ludlow), *Ae. sierrensis* (Ludlow), *Ae. vexans* (Meigen), *Culex erythrothorax* Dyar, *C. peus* Speiser, *C. pipiens* L., and *Culiseta inornata* (Williston).

from the release site. CO_2 traps recaptured 22 mosquitoes—nearly 85 per cent of the 26. In addition, one marked specimen was recaptured in a light trap on Night 1 at the maximum recapture distance of 0.43 mile, and three specimens were recaptured in resting boxes, set out for comparison with the CO_2 traps. One CO_2 trap only 65 feet from the release site captured two marked females on Night 3.

1961 Experiments

In the third summer (table 3) four releases were made in rice and the rest in other agricultural areas. There was little or no wind on the nights of the first six releases, and some specimens were recaptured in all quadrants. However, 95.6 per cent of the recaptures on those nights were found in the southeast quadrant, leading us to believe that the general movement of the females of *C. tarsalis* was into the wind. We learned otherwise when we released mosquitoes on August 29. A wind of 3–5 mph caught a large number of individuals as they rose from the holding cage and carried them across the road and over nearby trees; they disappeared downwind. Other individuals remained near the ground and flew upwind, at a low level, into an adjoining alfalfa field. Probably many found shelter and did not disperse at all in so strong a wind.

Mosquitoes were released on August 28, 29, and 30 in an alfalfa field 3 miles north of the center of Woodland (i.e., 2 miles from the city limits). On each release night we placed eight traps in the city, upwind, and two to seven other traps nearer the release point, both upwind and downwind. Two of the nine recaptures were made within the city proper at a distance of 2.75 miles upwind, one on Night 0 and one on Night 3.

The release of September 5 was made in an agricultural area 4 miles southeast of the center of Woodland, with a very light wind blowing toward the city. Traps were placed in circles 1, 2, and 3 miles from the release point. On Night 0, one mosquito was recaptured 2.2 miles downwind and 11 others in semirural areas in all quadrants in the 1-mile circle. Only two of the 15 recaptures in three nights were taken in the city. Either there was no strong tendency for the mosquitoes to fly toward the city lights and scents or the individuals that reached the city were less attracted to the CO_2 traps than to the available people, animals, and poultry.

The final release—made on Septem-

TABLE 3

RELEASE-RECAPTURE EXPERIMENTS, 1961

Culex tarsalis, females

Date	Release data: Weather at release site: Wind	Release data: Weather at release site: Temperature	Release data: Marked mosquitoes	Mosquitoes recaptured: Night 0	Mosquitoes recaptured: Night 1	Mosquitoes recaptured: Night 2	Mosquitoes recaptured: All nights	Significant recapture data: Distance	Significant recapture data: Direction	Significant recapture data: Night	CO_2 traps: Number and arrangement	CO_2 traps: Approximate distance from release site	Additional catch: *C. tarsalis*, unmarked
	mph	*°F*	*approx. no.*	*no.*	*no.*	*no.*	*no.*						*no.*
6/24	0	98	1,100	39	31	21	91	180 yd.	UW	0	6, UW, CW	40–180 yd.	1,816
7/5	0	74	3,000	7	0	0	7	200 yd.	UW	0	13, in circles	50–200 yd.	23,154
7/19	2	90	6,000	88	0	—	88	0.75 mi.	UW	0	18, all quad.	0.25–0.75 mi.	31,521
8/2	0	76	3,000	0	0	—	0	—	—	—	18, UW, CW	0.5–2.0 mi.	6,536
8/20	0	88	3,400	3	4	1	8	1.5 mi.	UW	0	20, mostly UW	0.5–1.5 mi.	32,326
8/28	2–3	76	5,000	0	—	—	0	—	—	—	10, UW, DW	0.75–4.0 mi.	310
8/29	3–5	79	5,000	0	—	—	0	—	—	—	10, UW, DW	0.75–4.0 mi.	320
8/30	0–3	76	4,000	8	—	—	9*	2.75 mi.	UW	0	15, UW, DW	0.75–4.0 mi.	880
9/5	0.75	81	4,000	12	1	2	15	1.0 mi.	All dir.	0	19, in 3 circles	0.5–3.0 mi.	6,082
								2.2 mi.	DW	0			
								3.0 mi.	DW	1			
9/11	0	81	6,000	3	2	0	5	2.0 mi.	DW	0	20, in 1 circle	2.0 mi.	3,002
								2.0 mi.	CW	0			

* Including one marked specimen taken in the city on Night 3.

NOTE: UW = upwind quadrant; DW = downwind quadrant; CW = crosswind quadrants (either or both).

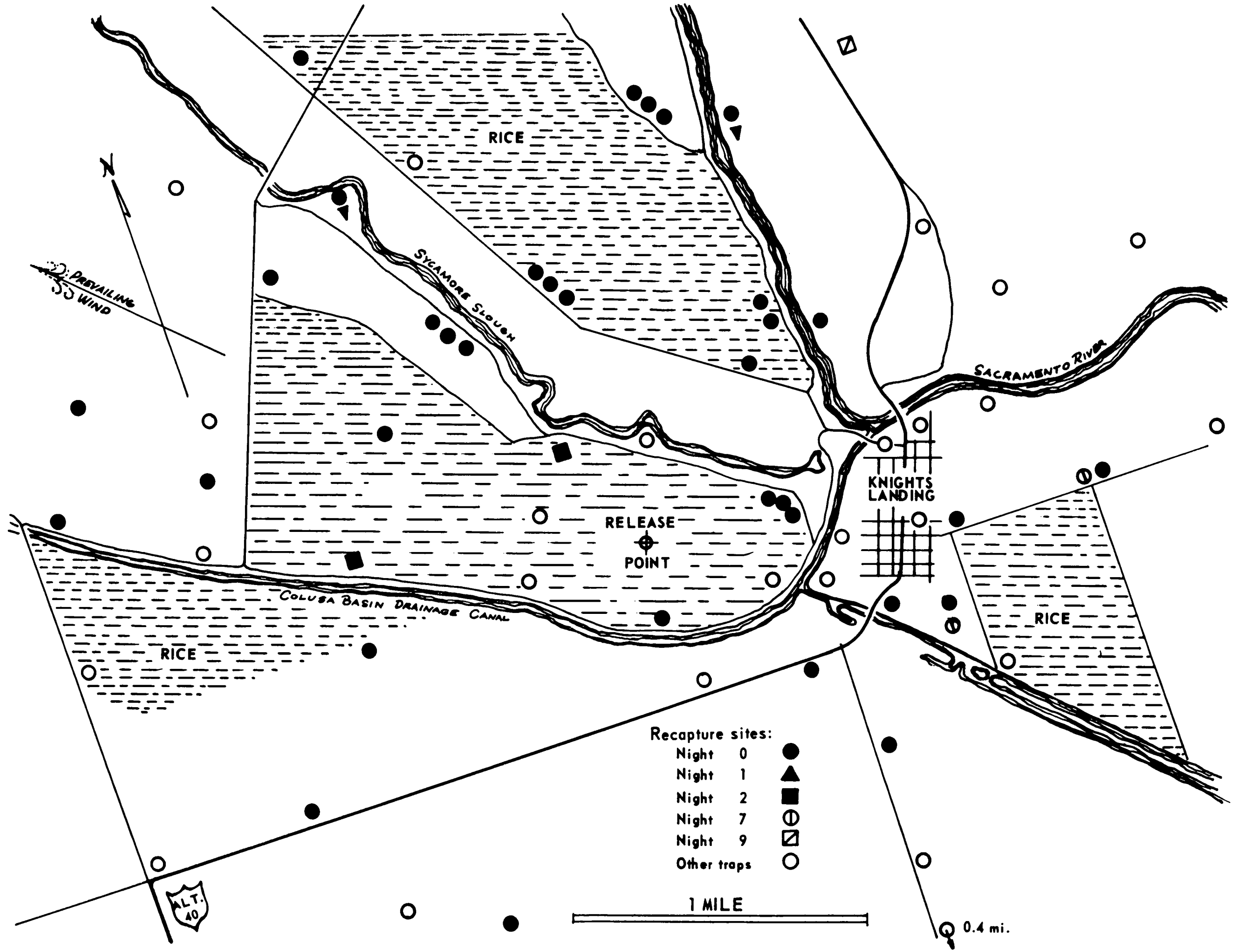

Fig. 8. Experimental area of June 19, 1962, showing trap positions in circles around the release point, on radii of approximately 0.5, 1.0, 1.5, and 2.0 miles.

ber 11, with no wind, 2 miles south of the September 5 release site—again yielded recaptures 2 miles away, north and east, on two nights. There was no town within the 2-mile radius, where traps were placed.

During the season, 72 per cent of the recaptures were made on Night 0, 17 per cent on Night 1, nearly 11 per cent on Night 2, and 0.4 per cent on Night 3.

1962 Experiments

The fourth season (table 4) was the most successful of the entire project. Besides gaining experience in trapping techniques, we had learned to relate our experiments to the local wind patterns. We made a release almost every week and recaptured marked specimens in all but one experiment. When we set traps for Releases 2 and 3 in the same spots as the traps for Releases 1 and 2, we caught a few specimens marked with the color used the preceding week and found that not all of the mosquitoes had left the immediate area where they were released. The five delayed recaptures made up nearly 2 per cent of the season's 254 recaptures. Of the other recaptures, 79 per cent were taken on Night 0, 15.4 per cent on Night 1, and 3.6 per cent on Night 2.

Wind velocities were considerably higher than in the two preceding seasons, and most of the recaptures were made downwind. Since many mosquitoes released in a wind were blown beyond those traps that were placed near the release site, we attempted trapping at greater distances than before and also concentrated our recapture efforts in the upwind and downwind quadrants primarily. The maximum distance of recovery in 1962 was 9.3 miles on Night 2 following the release of August 14.

After the first release, on June 19, in a rice field near Knights Landing, the 2-mph wind died down completely in about half an hour and was negligible during the remainder of the night. With this slight wind, the mosquitoes dispersed in all directions on Night 0, and some flew at least 2 miles with little aid from the wind. Figure 8 shows the locations of the recaptures and of the 54 traps, placed in concentric circles around the release site and approximately half a mile apart—as nearly as access roads permitted.

On June 26 we made simultaneous releases 3.8 miles apart, with 4,500 mosquitoes 2.6 miles downwind from the center of Knights Landing and 5,500 mosquitoes marked with a different color 1.2 miles upwind from the center of town. Again we placed traps in concentric circles approximately half a mile apart, but this time the release points were on the outer circle, opposite one another. No mosquitoes were recaptured in town, nor did individuals from the two release points overlap in their recapture patterns, even after eight nights. The wind velocity averaged 4.02 mph during the evening, yet two of the recaptures on Night 0 were upwind—0.5 and 1.0 mile from the release point. Winds were very light on Nights 1 and 2 and again the recaptures were upwind, to 1.25 miles.

Marked mosquitoes released July 3 at the site of the June 19 release were recaptured in all quadrants—one individual almost directly upwind, 0.7 mile from the release site. Traps were arranged as in the first experiment. By coincidence the wind velocity at release time was the same as that of June 26. The majority of the marked mosquitoes dispersed with the wind, but one individual was recaptured in the center of town, 1.5 miles east of the release site, on Night 2.

The release of July 10 was made in the northern part of Knights Landing. Traps were distributed throughout the town and the surrounding farming area in all quadrants, to a maximum distance of 3 miles. The breeze of 2 mph at the release site gave the mosquitoes ample opportunity to receive the odors of various animals, both human and domestic, but at the field weather station about three fourths of a mile to the east the

TABLE 4

RELEASE-RECAPTURE EXPERIMENTS, 1962

Culex tarsalis, females

Date	Release data			Mosquitoes recaptured				Significant recapture data			CO_2 traps		Additional catch: *C. tarsalis*, unmarked
	Weather at release site		Marked mosquitoes	Night			All nights	Distance	Direction	Night	Number and arrangement	Approximate distance from release site	
	Wind	Temperature		0	1	2							
	mph	*°F*	*approx. no.*	*no.*	*no.*	*no.*	*no.*	*mi.*				*mi.*	*no.*
6/19	2.12	90	3,600	32	2	2	39*	1.5 2.0	UW, CW DW	0 0	54, in 4 circles	0.5–2.0	29,616
6/26	3.57	72	10,000	6†	1	1	10*	1.0 2.0 2.0	UW DW UW	0 8 9	54, in 4 circles	0.5–3.8	23,620
7/3	3.57	75	9,500	61	4	3	68	2.0 1.0 1.5	DW UW CW	0 1 2	54, in 4 circles	0.5–2.0	40,890
7/10	2.01	81	2,000	5	1	—	6	1.0	CW	0	54, all quad.	0.25–3.0	37,929
7/17	5.43	76	20,500	0	4	0	4	2.25	UW	1	54, in arcs, UW	2.0–6.25	37,116
7/24	8.00	75	18,000	2	7	2	11	3.0 1.0 1.25	DW UW CW	0 2 2	54, in circles	1.0–3.4	30,305
7/31	9.10	74	11,000	0	1	0	1	5.25	DW	1	54, arcs UW, DW	5	23,299
8/14	1.70	73	28,400	47	14	1	62	5.0 9.3	DW DW	0 2	50, DW	0.5–12.0	39,394
8/21	6.50	74	12,000	0	—	0	0	—	—	—	55, DW	0.25–19	14,155
8/28	4.90	76	13,500	13	—	—	13	1.2	DW	0	54, UW, DW	0.8–1.2	4,373
9/5	1.00	74	5,500	22	4	—	26	0.6 0.5	DW CW	0 1	42, in circles	0.1–1.0	8,276
9/11	1.90	76	6,200	13	1	—	14	2.8	DW	0	31, UW, DW	0.6–3.0	10,250

* Recaptures on nights 7, 8 and 9 are explained in text.
† One of these specimens was taken in a light trap.
NOTE: UW = upwind quadrant; DW = downwind quadrant; CW = crosswind quadrants (either or both).

wind was 4.25 mph. On Night 0, mosquitoes were recaptured in all quadrants—two at the edge of the residential area and three others out of town. This experiment showed that not all blood-hungry mosquitoes remained in the community, even though there were domestic chickens—one of their preferred hosts—within 50 feet of the release point. Probably many of the released mosquitoes found warm-blooded hosts in preference to the CO_2 traps in town. Nevertheless, the dispersal pattern was not significantly different from the usual recaptures of mosquitoes released in unpopulated areas, i.e., in all quadrants when wind velocity was low.

The fifth release, on July 17, was made between two safflower fields in the center of the rice area. The traps were all upwind, in a series of arcs with a maximum angle of 92°. No mosquitoes were recaptured on Night 0, probably because of the strong wind, but on Night 1, which was calm, we recaptured four mosquitoes almost directly upwind.

On July 24 there was a strong wind, varying from ESE to SE, which dropped to zero after half an hour and remained negligible (0.5 mph) the next two nights. In this experiment we released 2,000 mosquitoes tagged with radioactive P^{32} and 16,000 marked with Helecon dust in the center of a rice field. None of the radioactive specimens were recaptured. Helecon-dusted individuals were recaptured 1 to 3 miles downwind from the release site on both Night 0 and Night 1. The recaptures on Night 2 were 1 mile upwind and 1.2 miles northeast from the release site.

Wind velocity on July 31 (9.1 mph) was the highest for any release night. All the traps were placed in the rice area, in arcs approximately 5 miles from the release site, in the upwind and downwind quadrants. The wind added to the distance made a very severe test, especially as we had not obtained a large number of mosquitoes for this experiment. Probably many of the specimens found shelter after their release and did not disperse in this high wind, and others may have been blown beyond the 5-mile traps. The single recovery was made on Night 1, when the wind was only 0.7 mph.

The eighth release, on August 14, was one of the most significant. We released more mosquitoes than in any other test and recaptured 62 of them in three nights. The release site was half a mile from the highway, at the edge of a grain-stubble field. There were occasional fields of alfalfa, safflower, sugar beets, and tomatoes distributed among the rice fields, and there was no concentrated residential area. All traps were in the downwind quadrant. Figure 9 shows that most of the recaptures were made in an area of flat terrain and rather directly downwind from the release site. The recapture at a distance of 5 miles on Night 0 is a record for the entire project, and the four later recaptures at 8.5 to 9.3 miles are significant. On Night 0 the closest trap, 0.6 mile west of the release site, recaptured 24 mosquitoes and a trap 2.8 miles northwest recaptured seven. The following records on the recaptured specimens indicate that the released mosquitoes scattered more widely each night in this open terrain at low wind velocities.

NIGHT	WIND (8–12 PM)	MARKED MOSQUITOES	DISTANCE FROM RELEASE SITE		
			MINIMUM	MAXIMUM	AVERAGE
	mph, av.	*no.*	*mi.*	*mi.*	*mi.*
0	2.9	47	0.6	5.0	1.25
1	0.8	14	0.5	8.75	5.25
2	0.0	1	. . .	9.3	. . .

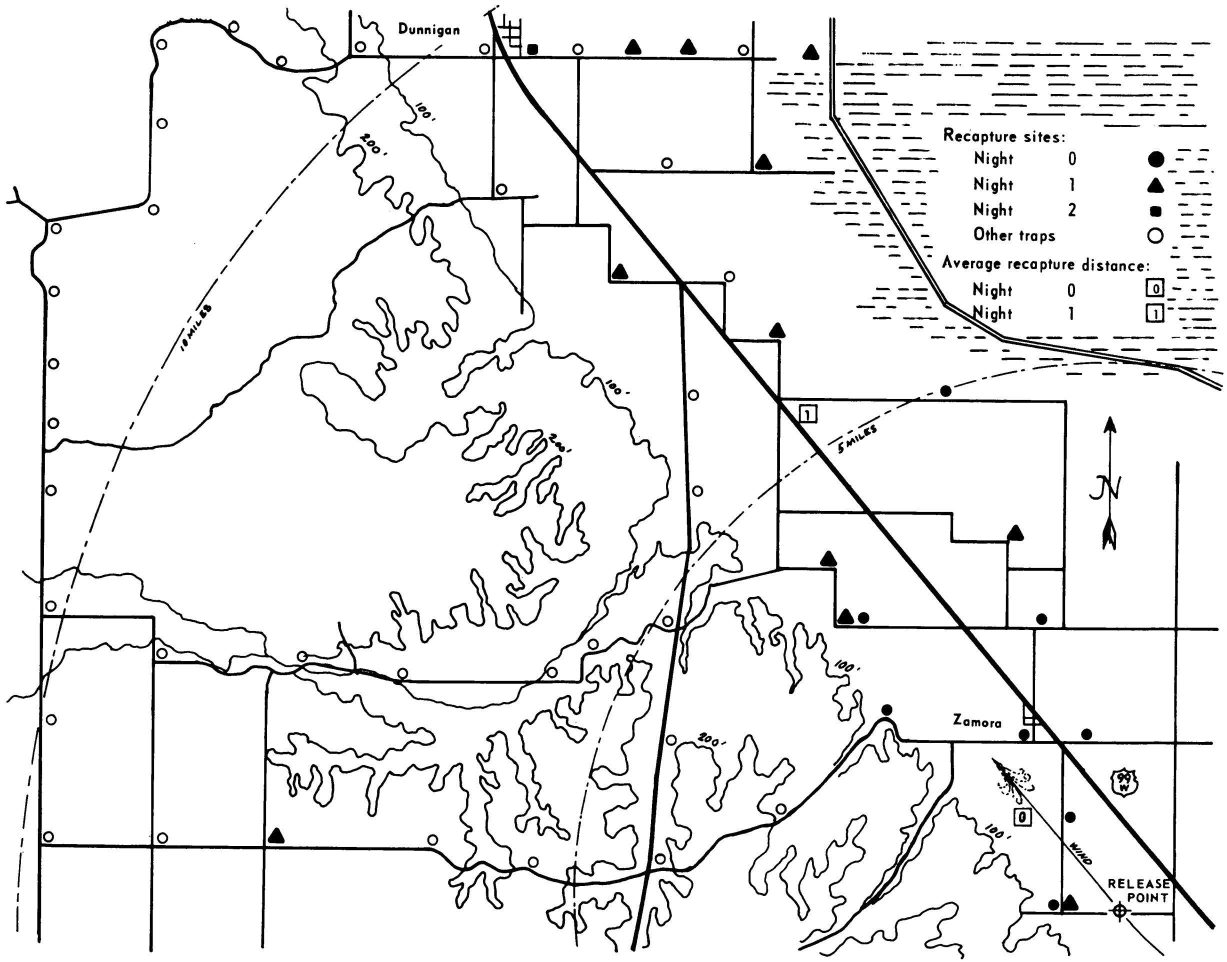

Fig. 9. Experimental area of August 14, 1962, showing trap positions—all in the downwind quadrant.

The average distance of recapture may be assumed to represent the center of dispersal, and this distance was extended each night. For the 62 recaptures in three nights the average is 2.5 miles. As the dispersal area widened each night, the recaptures were in reality good fortune for the experimenters.

The release of August 21, also in an area of general agriculture, gave no recaptures. Several mosquitoes flew a few feet against the 6.5-mph wind before it caught and carried them away. Traps were set on Nights 0 and 2. Most of the traps were placed in arcs from 11 to 19 miles downwind; only single traps were placed at 3.5, 5, and 10 miles downwind and 0.25 mile west from the release site.

The release of August 28 is described under Speed of Travel, page 98.

The CO_2 traps in the rice fields did not supply very large numbers of mosquitoes for the September experiments. On September 5 we released two small lots of mosquitoes in the center of Knights Landing, principally to test the retentiveness of metallic bronzing powder under field conditions. Results are discussed under Marking, on page 79. On Night 0, with winds of 1 mph or less in town and of 4.2 mph or less at the field weather station, 12 mosquitoes were recaptured downwind and 10 crosswind—all at short distances from the release point. It is possible that most of the mosquitoes failed to detect the traps readily because of the density of buildings and shrubbery.

The last release of the season, on September 11, was designed to test an observation that *C. tarsalis* females tend to fly along sloughs and other waterways and near the ground level. Marked mosquitoes were released just above the water of Sycamore Slough—a natural, treelined channel meandering in a general southeast direction and draining into the Sacramento River near Knights Landing. The prevailing wind follows the channel, blowing upstream. Wind velocity 5 feet above the edge of the water at the release site was 1.9 mph; on the bank, 15 feet above the water, it was 4.9 mph. Traps were placed at ground level along the banks of the slough to a distance of 3 miles both upwind and downwind. All the recaptures were made downwind.

In various ways the 1962 data indicate that released females of this species, supposedly seeking blood, tend to disperse for short distances in all directions when wind velocity is low but, more usually, to travel with the wind—even when there are preferred hosts and shelter nearby. The dispersal spreads over a wider area during each of the first few nights. However, there are also some individuals that do not scatter but remain near the release site.

1963 Experiments

In the last summer of the flight-range project, the weather was much cooler than in any of the other four years. The cumulative temperature for June, July, and August was 9.3° F below normal. Because of such low temperatures it was difficult to obtain large numbers of mosquitoes for the experiments. Only 0.11 per cent of the released mosquitoes were recaptured—largely because we were extending the trap range to greater limits than before. Possibly the cold nights reduced the potential catch by making detection of the CO_2 less probable and by lowering the mosquitoes' flight activity. No recaptures were obtained from three of the experiments, two of which were very severe tests with high odds against recapture. Moreover, the total catch of unmarked mosquitoes was very low. In five of the seven experiments the numbers of wild mosquitoes caught in one or two nights were lower than the numbers of marked mosquitoes released.

Table 5 summarizes the 1963 experiments. The first release, on July 9, was an attempt to determine the rate of dispersal in a diversified farming area near Cache Creek, with orchards, many farm buildings, and the small communities of Zamora and Yolo. The wind

TABLE 5

RELEASE-RECAPTURE EXPERIMENTS, 1963

Culex tarsalis, females

Date	Release data			Mosquitoes recaptured				Significant recapture data			CO_2 traps		Additional catch: *C. tarsalis*, unmarked
	Weather at release site		Marked mosquitoes	Night			All nights	Distance	Direction	Night	Number and arrangement	Approximate distance from release site	
	Wind	Temperature		0	1	2							
	mph	*°F*	*approx. no.*	*no.*	*no.*	*no.*	*no.*	*mi.*				*mi.*	*no.*
7/9	1.8	79	9,450	0	0	—	0	—	—	—	52, in a circle	5	8,415
7/16	2.4	79	4,000	16	—	—	16	1.3 0.4	Down canyon Up canyon	0 0	39, in a 4-mi. line, in canyon	0.1–3.3	558
7/22	4.3	74	14,000	—	0	1	1	15.75	DW	2	100, DW, in a 10-mi. line	13.5–17.5	23,196
7/30	2.7	84	17,000	12	—	—	12	2.1	UW	0	21*, UW, in a 2-mi. line	1–2.25	707
8/6	4.3	78	11,500	48	—	—	48	2.25 1.6	DW UW, CW	0 0	100, in a 3-mi. square	1.5–2.25	5,269
8/13	1.3 1.2	81 76	5,000 4,000	—	0	0	0	—	—	—	100, DW, in a 5-mi. line	16.75–20	20,568
8/20	7.6	82	2,900	0	—	—	0	—	—	—	20, DW, on Bald Mtn.	3–5.5	413

* The 21 traps were replaced twice during the evening, but the fresh traps were set in the same 21 locations.

NOTE: UW = upwind quadrant; DW = downwind quadrant; CW = crosswind quadrants (either or both).

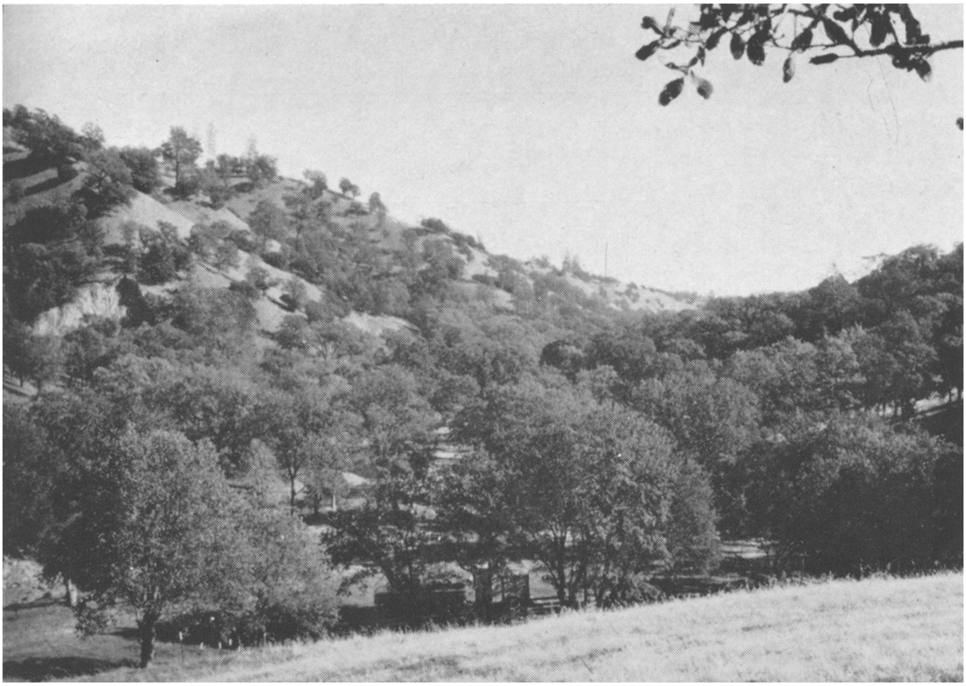

Fig. 10. Upper, western end of Oat Creek Canyon in northwestern Yolo County. A release was made here on July 16, 1963, in the foreground area at 520 feet elevation.

dropped from 1.81 mph at the time of release to less than 1 mph the remainder of the evening. In two nights no marked mosquitoes reached the traps, in a circle 5 miles from the release site. There were many obstacles to dispersal in the area, as well as many resting sites and competing hosts.

The experiment of July 16 showed that, on a single evening, *C. tarsalis* may move readily—with the vagaries of the evening breezes—both up and down the canyons on the west side of the Sacramento Valley, if this mosquito happens to reach the area. At 8:40 PM we made two releases, simultaneously, in a typical wooded canyon with oak and brush. We released 2,000 mosquitoes at 520 feet elevation (fig. 10), where the canyon forked into more open terrain at its upper, western end, and another 2,000 mosquitoes, marked with a different color, at about 400 feet elevation, near the lower, eastern end of the canyon, 1.3 miles from the upper site. We distributed traps along a 4-mile east-west line, between and beyond these two sites. The wind in the canyon area during the early evening was variable in direction, with a velocity of 0 to 4 mph. Specimens from the upper release site were recaptured at far as 0.4 mile up the canyon and 1.3 miles down the canyon. Specimens from the lower site were recaptured as far as 0.4 mile up the canyon and 1.1 miles down the canyon. One marked female of *Aedes melanimon* Dyar was recaptured 1.6 miles up the canyon from the lower release site, when it attempted to bite one of the authors at a shaded spring the morning after the release. The total catch was low, as might be expected in a dry canyon about 6 miles crosswind from the nearest rice field. We feel that a larger number of traps, such as we were able to place in the more accessible valley areas, might extend the known natural range of *C. tarsalis* into the hills and farther from the breeding sites.

TABLE 6

INDIVIDUAL TRAP CATCHES OF *CULEX TARSALIS**

(Nights 1 and 2 following release of July 22, 1963)

Location and ground cover	Date	Number of mosquitoes											
		Trap 1	Trap 2	Trap 3	Trap 4	Trap 5	Trap 6	Trap 7	Trap 8	Trap 9	Trap 10	Total	Av.
Westernmost mile: Dry fallow or grain stubble	July 23	11	52	108	134	382	249	189	88	104	91	1,408	141
	July 24	28	27	17	19	86	109	70†	105	70	55	586	59
												1,994	99.7
		Trap 46	Trap 47	Trap 48	Trap 49	Trap 50	Trap 51	Trap 52	Trap 53	Trap 54	Trap 55		
Central mile: Irrigated crops and grain stubble	July 23	78	6	10	71	100	197	57	60	66	19	664	66
	July 24	131	163	81	107	36	39	66	137	80	25	865	86
												1,529	76.5
		Trap 91	Trap 92	Trap 93	Trap 94	Trap 95	Trap 96	Trap 97	Trap 98	Trap 99	Trap 100		
Easternmost mile: Chiefly rice fields	July 23	6	47	15	184	15	238	46	293	322	77	1,243	124
	July 24	100	246	302	59	54	21	247	325	3	422	1,779	178
												3,022	151

* Part of data from 100 CO_2 traps set in a 10-mile east-west line, showing variations in catch from trap to trap and from night to night. Wind SSE, averaging 3.5 mph during Night 1 and 0.3 mph during Night 2.

† Location of the single recapture, 15.75 miles downwind from release point (see table 5).

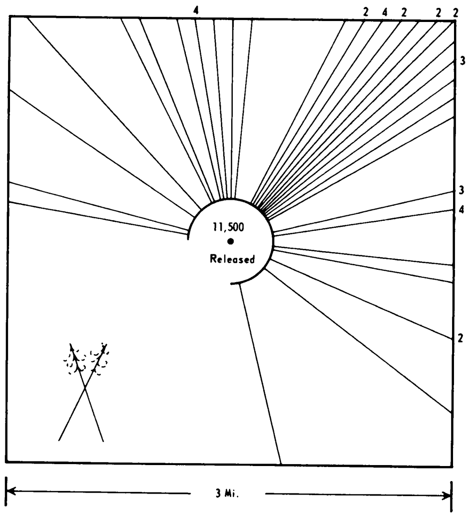

Fig. 11. Pattern of dispersal of *Culex tarsalis* on August 6, 1963, at Madison, California. Lines indicate direction from the release point to the traps that recaptured marked mosquitoes, with one to four marked specimens per trap.

For the third experiment, on July 22, we set out 100 traps (table 6) instead of the usual 20 to 50 and placed them about 0.1 mile apart in an east-west line 10 miles long and 13.5 to 17.5 miles downwind from the release site—the next-to-greatest recapture distance attempted. This test gave the greatest distance record known for the species. The one mosquito recaptured was caught on Night 2 in a trap 15.75 miles downwind. A study of the catch of wild mosquitoes in this large number of traps shows how much variation there is from trap to trap on one night and—at a given site—from one night to the next.

The release of July 30 is discussed under Speed of Travel, page 98.

On August 6 we made another attempt to observe the dispersal pattern by trapping in all directions around the release site, hoping for better results than we had from the July 9 experiment of this type, in different terrain. We released mosquitoes 4 miles southeast from the town of Madison, at the center of a 9-square-mile area which was flat and practically devoid of windbreaks except for a few farm buildings. There were no settlements, no orchard crops, no creeks or rivers. The largest acreage was in alfalfa, followed in order by fallow and stubble, sugar beets, tomatoes, safflower, irrigated pasture, and one rice field. Along the 3 miles of road on each side of the square we hung 25 CO_2 traps, 4 or 5 feet above the ground, on posts or poles or fences, at intervals of about 200 yards. Figure 11 shows the results. We recaptured 48 marked specimens, only six of them in the upwind or crosswind quadrants. The wind was mostly from the south, fluctuating from south-southeast to south-southwest and averaging 4.4 mph during the evening in this area. This experiment brought out a number of significant observations. The crops in this area did not filter out the dispersing mosquitoes or prevent their movement across the fields, as the trees and buildings seemed to do in the larger area of the first release. A few individuals were able to fly into a 4-mph wind, at least at low levels, but most of the mosquitoes were carried downwind.

One marked female of *Anopheles freeborni* was recaptured at a distance of 2.2 miles from the release point. Ten other females of this species were recaptured in the course of the 1961–1963 study.

The last two experiments gave negative results, in that no marked mosquitoes were recaptured. On August 13 we released relatively small numbers of mosquitoes at two points about 13 miles apart—one near the foothills at Capay and the other in the valley east of Yolo. The wind was only slightly more than 1 mph. Again we used 100 traps, all placed downwind in a 5-mile east-west line 16.75 to 20 miles from either release site. We set out traps on Nights 1 and 2 but not on Night 0. No marked mosquitoes were recaptured at this distance under these conditions.

The last release, on August 20, was an even more severe test. Six traps were placed along the ridge of Bald Mountain, elevation 1,820 feet (fig. 12), and 14 on its eastern slope, over a distance

Fig. 12. Northwestern Yolo County from Bald Mountain, elevation 1,820 feet. The trap in this location caught three females of *Culex tarsalis* on the cool, windy evening of August 20, 1963.

of 4 miles. We released a small number of marked mosquitoes in the Capay Valley at 299 feet elevation, about 3 miles southwest of the peak. From there a strong wind was blowing directly toward the peak at 7.6 mph at ground level in the valley and at much higher velocity on the mountain. Although no marked specimens were recaptured, it was significant that 38 unmarked females of *C. tarsalis* were caught in the windy locations on the ridge itself and another 375 in the more sheltered locations on the eastern slope of the ridge (the lee side, away from the release site). The mosquito does not breed within about 8 miles of this isolated area, as far as we could ascertain, yet it appears to move there freely, regardless of elevation—presumably brought by the wind from the valley.

Dispersal Upwind From Rice Areas

In two trapping experiments we analyzed the natural upwind flights of *C. tarsalis* from rice areas. On July 11, 1961, a warm evening with little wind, we placed 14 CO_2 traps in a north-south line (table 7) that started in a rice field north of Knights Landing and extended 3.75 miles upwind, through the diverse field crops grown in the county, and into the town of Knights Landing. The largest catches were in the rice area. Beyond 3 miles upwind from the breeding area (in traps 2.5 miles from the edge of the rice field) the catches dropped noticeably. The catch was characteristically low in a castor bean field, as mosquitoes seem to avoid this crop. Otherwise we found only the usual variations in individual trap catches.

We set traps 15 days later (table 8) on a much cooler evening, with a southeast wind averaging 4.5 mph. The line of 13 traps started at our field weather station at the edge of a rice field and extended 11.5 miles upwind to the city of Woodland. The mosquito abatement district had done intensive control work in this area, and we know of no breeding sites other than those in the rice fields, where only a low level of control is possible. There were no rice fields upwind from Woodland. The average catch for all traps was less than one fourth of that on the warm, calm evening, and the distance from rice was four times

TABLE 7

CO_2 TRAP CATCHES OF *CULEX TARSALIS* UPWIND FROM BREEDING AREA
(Knights Landing, California, July 11, 1961)

Trap and ground cover	Trap distance and direction from start in rice field	Number of mosquitoes captured
1, Rice	100 yds. E	495
2, Rice	200 yds. E	1,870
3, Rice	0.50 mi. E	451
4, Rice	0.75 mi. E	1,552
5, Rice	0.90 mi. E	1,080
6, Margin between rice and castor beans	1.00 mi. E	888
7, Castor beans	1.25 mi. E	225
8, Dry weeds near slough	1.50 mi. E	534
9, Melons	1.75 mi. E	488
10, Grain stubble	2.25 mi. SE	357
11, Tomatoes	2.60 mi. SE	780
12, Melons	3.00 mi. SE	412
13, Safflower, dry margin	3.50 mi. SE	143
14, Residential	3.75 mi. SE	182
Total		9,457

NOTES: The average catch per trap was 1,056 in the rice area and 390 in other areas. The overall average was 675 per trap. Between 8:00 PM and midnight the average temperature was 83°F and the average wind velocity was 0.75 mph.

TABLE 8

CO_2 TRAP CATCHES OF *CULEX TARSALIS* UPWIND FROM BREEDING AREA
(Woodland, California, July 26, 1961)

Trap and ground cover	Trap distance and direction from edge of rice field	Number of mosquitoes captured
1, Edge of rice field	0	767
2, Dry weeds, slough bank near rice field	1.75 mi. SSE	367
3, Alfalfa, recently cut	2.5 mi. S	40
4, Beans	3.0 mi. S	56
5, Tomatoes	4.25 mi. S	126
6, Alfalfa	5.0 mi. S	214
7, Milo	5.5 mi. S	164
8, Oak trees, dry camp ground	6.75 mi. SSE	39
9, Gravel, dry creek bed	7.5 mi. S	24
10, Grain stubble, dry	8.5 mi. S	73
11, Alfalfa, old and dry	9.25 mi. S	23
12, Lawns and shrubs, NE part of city	9.75 mi. S	116
13, Lawns and shrubs, SE part of city	11.5 mi. S	106
Total		2,115

NOTES: The average catch per trap was 567 in the rice area, 120 in irrigated crops, 111 among city residences, and 40 on dry ground. The overall average was 163 per trap. Between 8:00 PM and midnight the average temperature was 68.5°F and the average wind velocity was 4.5 mph.

as great. The two traps near the rice field caught more mosquitoes than the other 11 traps together, but catches in the residence areas were not significantly different from those in irrigated crops other than rice. The average catch in dry locations was only a quarter of the average for all 13 traps.

OTHER EXPERIMENTS

Speed of Travel and of Flight

We recorded time and distance in two special recapture experiments with *C. tarsalis* in the field. On August 28, 1962, before sunset, we placed 54 CO_2 traps along a road in the rice-growing area, about 60 feet apart in a north-south line about 0.6 mile long. At 8:15 PM (half an hour after sunset) we released 6,500 marked females at Site A, 1 mile upwind from the center traps. Simultaneously we released 7,000 females, marked with a different color, at Site B, 1 mile downwind from the center traps. As the line of traps was not quite at right angles to the wind direction, the distance from Site A to the several traps varied from 0.8 to 1.2 miles.

During the period of the experiment the wind blew from the southeast at an average velocity, on the road, of 4.9 mph (range from 0 to 7.3 mph) and the temperature dropped from 76° to 70° F. We plugged and removed 18 traps (every third one) at 8:30 PM, another 18 at 9:00 PM, and the last 18 at 9:30 PM. The 54 traps captured 4,373 unmarked individuals of *C. tarsalis.*

In the 75 minutes allowed, no mosquitoes from Site B reached the traps against the wind, but the mosquitoes released from Site A fanned out so that 13 specimens were recaptured in 12 traps. Apparently they were able to orient themselves to the local source of CO_2 and quarter back against the wind in response to the bait. Records on the recaptures are as follows:

MARKED SPECIMENS	EXPOSURE INTERVAL	DISTANCE
no.	*min.*	*miles*
3	15	0.95—1.06
7	45	0.95—1.15
3	75	0.88—1.18

At least one mosquito from Site A was carried in flight 1.06 miles downwind within 15 minutes, and it is possible that most or all of the 13 recaptured mosquitoes reached the traps at about the same time. This experiment does not indicate the speed of actual flight, as all the recaptures were downwind from the release site.

We measured actual flying time on July 30, 1963, among dry, low, rolling hills covered chiefly with grain stubble and dry pasture, in the western part of the county about 10 miles from the rice fields. There was no known breeding site in the area and the total catch of wild mosquitoes was low. We spaced 21 traps 0.1 mile apart in an east-west line along a 2-mile stretch of road (fig. 13). At 9:00 PM (about twilight) we released 7,500 marked mosquitoes from Site A, 1 mile north of the center trap, and 9,500 mosquitoes marked with a different color from Site B, 2 miles north of that trap. After 20 minutes we plugged and removed the first 21 traps and placed a second set in the same 21 locations. Fifty minutes later we removed the second set and placed a third set, which we left until morning.

The evening was warm. During the first 20 minutes of the test the wind blew at a fairly constant velocity of about 2.7 mph but varied from south-southwest to nearly west. The remainder of the night the wind varied from 2.2 to 3 mph, still blowing from a westerly direction.

We captured four marked specimens from Site A within 20 minutes, two more during the next 50 minutes, and two more before morning. Before morning, also, four marked mosquitoes from Site B made their way to traps 2.1 miles upwind or crosswind. Every recaptured mosquito flew without help from the wind. Each of the first four flew approximately 1.3 miles in 20 minutes or less across a wind of 2.72 mph. By the method of vector analysis, as employed in physics, we calculated that their actual flying speed was at least 4.75 mph. However, we do not believe that such delicate insects would maintain a steady, sustained flight at 2 to 4 mph in

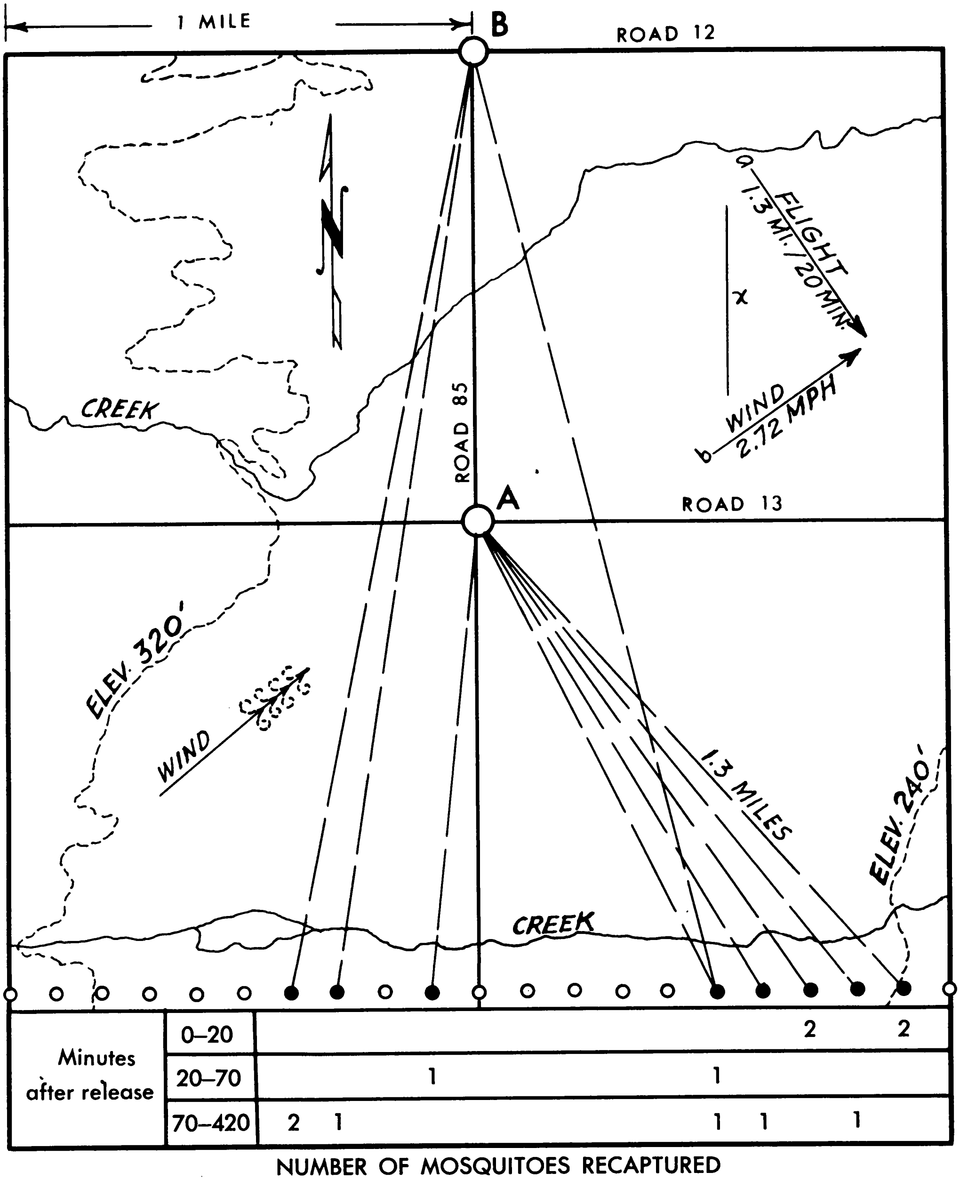

Fig. 13. Map showing release points (A and B) and trap arrangement in speed-of-flight experiment. Yolo County, California, July 30, 1963. Speed of flight, x, = $\sqrt{a^2+b^2} = \sqrt{3.9^2+2.72^2}$ = 4.75 mph.

one direction under their own power for periods of several hours, even if it were possible and if the weather conditions were favorable for flight.

We know of no other exact field measurements of flight speed for any mosquito species. Kennedy (1939) and Hocking (1953) have published data based on experimental laboratory flights of only a few feet. They reported average flight speeds of 3.3 mph for *Aedes aegypti* (Linnaeus), 5.6 mph for *Ae. flavescens* (Swellengrebel), and 5.0 mph for *Ae. impiger* (Walker).

Time of Flight and its Relation to Temperature

Observations made in the rice study area indicate that a definite peak of flight activity occurs during the first hour after twilight. On the evenings of the first two experiments described below, flight activity dropped rapidly after the first catch—i.e., within an hour after sunset. On the evening of the third experiment, August 30, 1962, the peak flight occurred between 52 and 82 minutes after sunset. In the fourth experiment the period of high catches again lasted into the second hour after sunset in the warmer location, but the same night in another trap—only 1 mile away and slightly cooler—it ended within 65 minutes after sunset.

All of the timed catches indicated some activity at almost any hour of the night when it was not too cold, but the first three experiments ended before morning. In the fourth experiment, at low temperatures, there was practically no predawn increase in catch. A fifth experiment, with a definite predawn peak catch, shows the temperature relationships rather clearly.

1. On July 16, 1962, a dark automobile was parked crosswind, with screen-cone traps taped over the two front windows. A man in the vehicle served as bait. The sun set at 8:29 PM. The experiment began shortly thereafter and continued until 2:00 AM. Most of the specimens captured were females of *C. tarsalis,* but there were also a few of *Anopheles freeborni.* No mosquitoes were caught on the upwind screen. The downwind screen gave the following mosquito counts: more than 300 at 9:30 PM, 20 at 10:30, none at 11:00, four at midnight, one at 12:30 AM, five at 1:00, and four at 2:00. Temperatures were 75° F at 9:00 PM, 71.5° at 10:00, 68° at 11:00, and 65° at 2:00 AM.

2. In the speed-of-travel experiment on August 28, 1962, traps placed before sunset—which was at 7:45 PM—were plugged and removed at 8:30, 9:00, and 9:30 PM (45, 75, and 105 minutes after sunset). The third catch of *C. tarsalis* (1,417 wild specimens) was less than the second (1,574) and not much more than the first (1,382). Although temperatures remained above 70° F throughout the experiment, the length of time traps were in place after 8:30 did not markedly increase the total catch.

3. We obtained a rather precise timing of flight activity over a rice field on August 30, 1962, by changing the traps every 30 minutes. The time of peak flight was a little later than usual. No mosquitoes entered the traps during the first 52 minutes after sunset, and the peak catch occurred very definitely in the following half hour, at temperatures between 76° and 68° F (5 feet above the rice). The sun set at 7:38 PM. The wind velocity was 3.1 to 4.7 mph at a height of 6 feet and up to 8 mph at a height of 20 feet. Details were as follows:

TRAPPING PERIOD PM	TEMPERATURE RANGE ° *F*	*Culex tarsalis* *no.*
7:00—7:30	80.0—77.5	0
7:30—8:00	77.5—76.0	0
8:00—8:30	76.0—70.0	0
8:30—9:00	76.0—68.0*	108
9:00—9:30	68.0—66.0	4
9:30–10:00	66.0—64.0	3
10:00–10:30	64.0—62.0	2
10:30–11:00	62.0—60.0	0
11:00–11:30	60.0— . . .	5

* Between 8:30 and 9:00 PM there was a temporary increase in temperature, followed by the usual downward trend.

4. On the night of August 19, 1963, we recorded the activity of *C. tarsalis* from 8:00 PM to 7:00 AM by trapping at two locations—one on a dirt road near the Sacramento River and the other 1 mile southwest, in a rice field. We changed both traps hourly and took the temperature hourly with a sling psychrometer at each location. The sun set at 7:55 PM and rose at 6:24 AM. The wind was light and variable, veering to the north before midnight and increasing somewhat—even briefly approaching 5 mph. The

location on the road was several degrees warmer than that in the rice field, especially before midnight, and the catch on the road was double the catch in the rice field. The evening peak of activity lasted considerably longer in the warmer location, but after 2:00 AM the catch in the rice field was slightly higher than that on the road. Because of the usual differences in catch at different locations on one night we cannot stress the relation of temperature in this one instance. Ordinarily, however, we would have expected to obtain the higher catch in the rice field. The temperature continued to drop until sunrise, to 59° or lower at both trap sites. At least one mosquito was caught every hour, but there was no appreciable predawn increase in catch. The following table gives the differences in temperature and in catch at the two locations:

TRAPPING PERIOD	RICE FIELD		RIVER ROAD	
	°F	*no. mosq.*	*°F*	*no. mosq.*
8:00— 9:00 PM	...—74.0	191	84.0—78.5	217
9:00—10:00 PM	74.0—69.5	1	78.5—77.0	173
10:00—11:00 PM	69.5—69.0	12	77.0—74.0	4
11:00—midnight	69.0—66.0	0	74.0—73.0	17
Midnight—1:00 AM	66.0—62.0	3	73.0—68.0	2
1:00— 2:00 AM	62.0—63.0	0	68.0—64.0	17
2:00— 3:00 AM	63.0—61.0	1	64.0—64.5	0
3:00— 4:00 AM	61.0—58.5	3	64.5—61.0	0
4:00— 5:00 AM	58.5—59.0	1	61.0—59.0	0
5:00— 6:00 AM	59.0—57.0	0	59.0—59.0	1
6:00— 7:00 AM	57.0— ...	3	59.0— ...	2
Total catch		215		433

5. On August 10, 1961, though the hours before midnight were not so warm as in the above experiment, the temperature dropped only slightly after midnight. The sun set at 8:07 PM and rose at 6:16 AM on August 11. The wind was slightly above 1 mph from 8:00 PM to 3:00 AM; from then until the end of the experiment it was variable at about 3 mph. We used one trap for each two-hour period. The catches at 2:00 and 4:00 AM were higher than those in the fourth experiment and the total catch was considerably higher. Also, with a minimum temperature of 67° F at about 5:00 AM, there was a definite predawn peak catch. For comparison with the data for August 19, 1963 (Experiment 4, above), the data for August 10, 1961, are as follows:

TRAPPING PERIOD	TEMPERATURE RANGE	CATCH
	°F	*no. mosq.*
8:00—10:00 PM	73—72	796
10:00—midnight	72—70	77
Midnight—2:00 AM	70—70	11
2:00— 4:00 AM	70—69	23
4:00— 6:00 AM	69—67	234
		1,141

The traps for all the above experiments were in the same general location in the rice-growing area.

Height of Flight

At dusk on August 8 and again on August 31, 1962, we suspended CO_2 traps from poles over rice, one trap at each height; we left them in place overnight. Total catches for the two nights were as follows: 42 females of *C. tarsalis* in traps at ground level, 94 at 5 feet, 304 at 10 feet, 36 at 20 feet, and 29 at 30 feet. On both evenings, shortly before the peak flights of the females, we observed males in swarms the tops of which were at least 30 feet above the ground.

On August 16, 1962, a Piper PA 11 aircraft flew at 80–85 mph ground speed over a rice area in which no control work had been done and exposed 15-inch screens smeared with Tanglefoot. The wind velocity 5 feet from the ground in the field sampled was 0–3 mph. Temperature was 80° F declining to 74°. The flight pattern was 7 miles in a northeast-southwest line. One screen was exposed at each height, with two passes (once across and return). The sun set at 7:38 PM. Starting at 8:13 PM the first screen, exposed at 25–30 feet above the rice, caught 150 mosquitoes; that at 50–60 feet caught 100; that at 80 feet caught one. Screens exposed at 100, 150, 400, and 500 feet caught no mosquitoes. Flights were completed at 9:05 PM. The majority of the specimens were *C. tarsalis*, but they were so embedded in the sticky surface that it was impossible to identify each one accurately or to determine the sex.

Fall and Winter Survey

During the fall and winter seasons of 1962–63 and 1963–64 we attempted to follow the movement of *C. tarsalis* females from the rice fields on the valley floor to their winter hiding places. We released no marked individuals but gathered our data from late September through March by field surveys and by counting mosquitoes in natural and artificial resting sites in the valley and in the hills both east and west of the valley.

In 1962–63 we found that, on the valley floor, semirural areas near Davis and Zamora yielded more specimens than residential areas in Davis and Knights Landing. This is true in summer also. In the hills we made two comparative studies: (1) Near Oat Creek in northwestern Yolo County (the location of the canyon experiment of July 16, 1963) we found no local breeding of *C. tarsalis*. The major rice acreage was 15 miles to the east, and in 1962 one small field 8 miles to the southeast was planted to rice. We placed four red boxes in brushy spots on the hillside—one each at 400, 600, 800, and 1,200 feet elevation —and collected their contents weekly, when weather and road conditions allowed, from December to March. Each box contained a temperature recorder.[10] The coldest location was at 600 feet. There was no freezing weather at 800 and 1,200 feet, but at 1,200 feet there were only nine days when the temperature went above 60° F. The 1,200-foot site was above the usual winter fog level in the valley. Since we removed all specimens at each visit and found others the next time, there evidently was some movement of mosquitoes at each location, even during the coldest months, though we found only a few specimens at 1,200 feet. In March we found no specimens at any of the stations. (2) At Gold Hill in Placer County, at 395 feet elevation on the east side of the Sacramento Valley, we collected under two two small bridges that crossed a ravine. In Earl Fisher's almond orchard in northwestern Yolo County, at the comparable elevation of 320 feet on the west side of the valley, we collected from a well house and two red boxes just outside. On comparable dates between October 17 and March 24 we made six collections at each of these two sites. We obtained more than three times as many specimens on the west as on the east side of the valley.

In 1963–64 we collected along State Highway 20 (an east-west route across the state) at scheduled sites, mostly under bridges, at eight elevations from 335 to 1,725 feet on the west side of the valley and at eight elevations from 268 to 2,640 feet on the east side. The closest rice fields the preceding summer were in

[10] Model 1000, Electric Autolite Co., Marshalltown, Iowa.

the valley—7 miles from the lowest collection site in the western hills and 5 miles from the lowest collection site in the foothills to the east. Between October 1 and February 25 we made eight trips in each direction. We obtained from 9 to 65 specimens per site on the west side and from 8 to 21 each at the three sites up to 395 feet on the east side. There were from 1 to 6 specimens each at the three east-side sites at 683 to 1,451 feet, none at 2,040 feet, and only two at 2,640 feet.

The experiments of July 16 and August 20, 1963, show that appreciable numbers of specimens could be found in the western hills in summer as well as in winter. In summer *C. tarsalis* females, seeking blood, may be attracted from a considerable area to one CO_2 trap. In fall and winter, when this mosquito feeds little or not at all, the CO_2 bait is ineffective and we had to depend on finding specimens in their natural resting places or in a few artificial sites (red boxes) that we established for the purpose. The red box is a resting station, not a trap. Hence, the catch at one particular time is much lower than that in any type of trap which baits and holds the specimens. As it was impossible to find more than a few of the many minute overwintering niches in the standard 15-minute collecting period at each site, we believe that the few specimens we were able to collect indicate the presence of a relatively large population. Although the counts recorded from isolated red boxes, from brush, and under bridges are low they are actually very significant and represent impressive numbers in terms of a square mile.

The only sites where we found any considerable concentration of *C. tarsalis* were the huge piles of flood debris at McCourtney Crossing on Bear River, 7.5 miles east of Wheatland at 207 feet elevation, in the fall and early winter of 1963. Mosquitoes flew out in impressive numbers when we trampled the brush piles, but they returned to their shelters almost immediately. The closest rice field was 6.5 airline miles southwest.

The collecting was no more abundant in the valley than in the hills. In the two winters we made 263 collections in the valley, with an average of 3.3 specimens per collection; 130 collections in the hills on the west side of the valley, with an average of 4.5 specimens each; and 69 collections below 1,700 feet in the Sierra foothills, east of the valley, with an average of 1.7 specimens each.

DISCUSSION AND CONCLUSIONS

Effect of Wind on Flight

The early experiments showed us that the direction and velocity of the prevailing winds were major factors in the dispersal of *C. tarsalis*. Once a mosquito is airborne the wind influences the direction and the distance of its travel. Some data on wind patterns in the Davis area, given on pages 75 and 76, show that mosquitoes moving with the prevailing winds in this area would be carried from the south or southeast toward the north or northwest on most summer evenings. Other parts of the Sacramento Valley might have different winds; we noted some variations in the wind pattern not far from our study area. Although the prevailing winds do not blow uniformly, either in velocity or in direction, the wind sweep in the flat, open type of terrain in the rice study area made for a wide dispersal of mosquitoes.

Knowledge of wind conditions to be expected at the time of a release and during the first four hours thereafter was of great importance in planning the trap placement for an experiment. The wind was southerly (SSE to SSW) on every release evening except for the speed-of-flight test on July 30, 1963, when it was SSW to nearly due west. It did not blow from the north on any of the evenings when we made releases. The strongest wind at the time of any

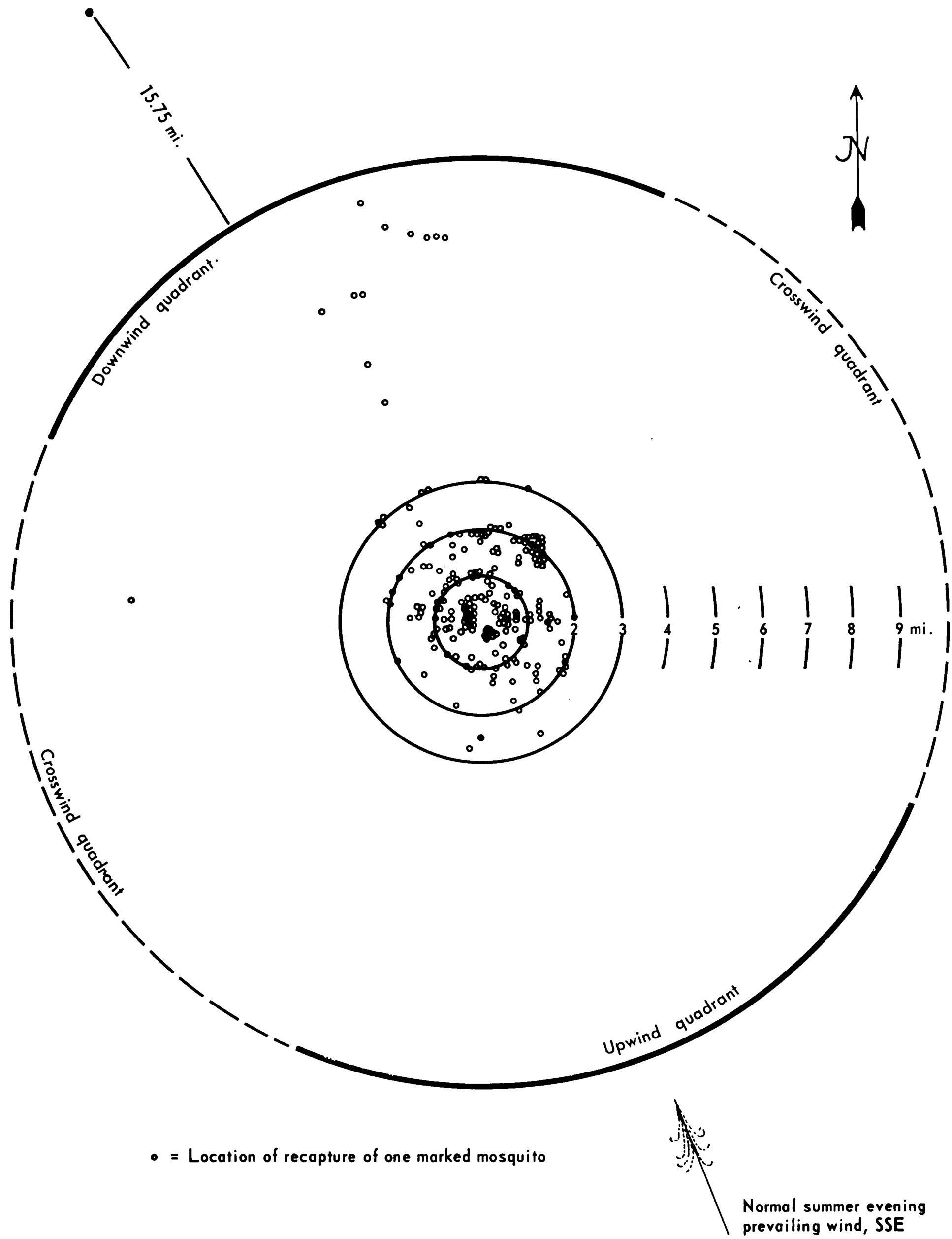

Fig. 14. Composite diagram of 18 release experiments with *Culex tarsalis* in the main rice area near Knights Landing, showing direction and distance of the recaptures. Yolo County, California, 1961–63.

release came from the south at 9.1 mph on July 31, 1962. Usually the wind diminished between 10 PM and midnight.

Figure 14 gives a schematic summary of the recaptures of *C. tarsalis* in 18 release experiments made in 1961, 1962, and 1963 in the valley proper, where the wind pattern is quite consistent. It depicts the effects of prevailing summer evening winds on the dispersal of this mosquito and shows some local and individual variations. It includes the early short-range tests but omits the two speed-of-flight experiments and the canyon experiment, none of which dealt directly with the distance and direction of dispersal, and it omits the experiment of August 6, 1963, because it was carried out in a different area, where the winds are more variable. Otherwise it shows all the recaptures during these three summers.

In our field work we observed a very consistent dispersal pattern. When swarms of mosquitoes of this species emerged from the rice fields in the early evening or were released from a holding cage, they would spiral upward in an irregular manner to heights of 12 or 15 feet, according to the temperatures of the atmospheric layers, and there would level off in the wind current. Most of them were caught by the wind sooner or later—immediately, if velocities were 5 mph or higher—and were carried over trees and other obstacles and often past the traps that were set at short range. However, this mosquito tends to head into the wind whenever possible. Even in the stronger winds, we observed that a few individuals remained near the ground and some worked their way for short distances upwind. Also, on several occasions, an individual was observed actually flying for a few feet into a 6-mph wind, about 3 feet above the ground.

Wind brings the scent of nearby hosts. Mosquitoes flying at low levels in rural areas often encounter wisps of wind, which may vary by the minute. The irregular odor trails so carried surely cause some individuals to move across the prevailing wind or to fly against winds of low velocity. Many times we observed that, when a noticeable breeze (e.g., 2–4 mph) was passing over a CO_2 trap, most of the mosquitoes that were traveling with the wind seemed to get the scent as they passed and quartered back, to return and enter the downwind end of the trap.

Eliason and Bailey (1962) constructed a wind-directional set of traps that rotates like a weather vane. In different locations and at different wind velocities the downwind traps regularly caught more mosquitoes than did the upwind traps, and the proportion increased with the wind velocity. During the 1962 season the downwind catch averaged four times as many mosquitoes as the upwind catch.

In the parked-automobile experiment of July 16, 1962, described under Time of Flight, the downwind trap caught more than 300 mosquitoes—mostly *C. tarsalis*—and the upwind trap caught no mosquitoes. The wind was light during the entire period and averaged 1.5 mph.

Conclusions about the effect of wind on the dispersal of *C. tarsalis* are based on all observations of the five seasons and especially on the records of recaptures on Night 0.

1. At low wind velocities, up to 2 mph, dispersal takes place in all directions. The greatest upwind distance of recapture was 2.75 miles, on August 30, 1961, against a wind of 0 to 2.9 mph.

2. At least 10 per cent of the mosquitoes from any particular release may disperse laterally, i.e., across the direction of the wind.

3. Above a limiting wind velocity of about 4 mph the general direction of dispersal is downwind. There is only very limited movement against or across a wind as high as 4 mph. No recaptures were made upwind when velocities were 5.4 mph or higher.

4. Wind velocities above 6 mph prob-

ably would not extend the distance of effective dispersal—i.e., the movement of significant numbers, which might become a nuisance or spread disease—because such high winds appear to discourage flight.

5. The swarms of males of this species exhibited very little horizontal movement and moved vertically only enough to remain in a breeze of slightly more than 2 mph. When the wind increased to 9 mph, even momentarily, the males dropped down behind trees, tall grass, levees, or even a parked automobile. When there was little wind the swarms were observed sometimes as high as 30 feet above the ground.

Effect of Temperature on Flight Activity

C. tarsalis is a temperate zone mosquito. We have observed it in flight at temperatures between 55° and 92° F during the evening hours of five summers. Our experiments were not designed to determine either the optimum temperature for flight or the limiting temperatures, and what information we gathered is a by-product of the basic flight-range study.

There is sometimes a tendency to oversimplify such an obvious activity as flight and to generalize that flight activity increases with a rise in temperature above a threshold for a given species. In general, we found the highest catches on evenings when temperatures remained above 65° F for two hours or more after twilight. However, the numbers of mosquitoes captured in CO_2 traps are determined by a combination of temperature and other factors—such as the trap location, the wind velocity and direction, and the numbers of blood-seeking mosquitoes emerging at the peaks of the several summer broods. Thus it is difficult to show the exact relation of the temperature factor in our data. We suspect that low catches, obtained sometimes on evenings with favorable temperatures, could have indicated the periods between peaks of emergence.

From the experience of many hundreds of trappings we make the following generalizations about the influence of temperature on the behavior of *C. tarsalis:*

1. Usually there is a definite reduction in flight activity below 65° F, but this is not a strict limit. At temperatures as low as 59° F small numbers of mosquitoes enter traps and an occasional individual has bitten an observer.

2. A combination of wind above 5 mph and temperature below 65° F discourages mosquito flight. Under these conditions we have observed large numbers of mosquitoes resting on grass, willows, posts, or other objects, and even on the outside of CO_2 traps set near the ground.

3. Activity increases with increase in temperature between 65° and about 75° F. Above about 75° there is little correlation between our trap catches and the temperature records of our weather station in the rice field. In our study area the temperature commonly drops below 65° F during a summer night, so that flight activity seems limited to the period between the end of twilight and the time when the temperature reaches approximately the 65° level.

Temperature inversion complicates the understanding of this question. At sundown after a hot day the air at the ground surface cools more rapidly than the air above, and this results in a stratification, so that there are more or less distinct layers of air, each at a different temperature, with the warmer air above—an inversion of the usual situation. The amount of heating during the preceding day affects the inversion rate. The mixing of these atmospheric layers depends on the strength of the prevailing wind from the coast and also on local shifts in wind velocity and direction. It occurs rapidly but at different rates over water, bare ground, irrigated crops, trees, etc.

Other investigators have reported how local conditions affect mosquito flight activity. Wellington (1944) observed the effect of the inversion phenomenon on *Culex* sp. in Toronto, Canada, and reported that "when the ground temperature was 60° F no males were present in the lower levels, but they were abundant at higher levels where the air temperature was 65° or more. . . . If the mean temperature of the air column dropped below 60°, no males were found, and females were present in the higher levels only." Pratt (1949) noted in Alaska that "Mosquito activity was greatest during inversion conditions, . . . except when the surface [ground] temperature was below 45° F. When the temperatures at body level were below 45° F and warmer temperatures were found above head level, many mosquitoes could be seen flying above one's head in the warmer air."

We made two attempts to measure the possible temperature inversions at 10, 20, and 30 feet above the ground in the rice area and to correlate these temperatures with trap catches at these heights, but our data were inconclusive. On evenings when the temperatures at these heights dropped below 60° or 65° F, few mosquitoes were seen above the ground cover but some would bite the observers' ankles. On such evenings we could see mosquitoes flying out of deep cracks in the dry, uncultivated soil at the margin of the rice area and occasionally reentering the cracks.

Time of Flight and its Relation to Temperature

Most mosquitoes are nocturnal, and their flight activity commences about dusk. The patterns of flight activity differ somewhat in the different species. Bates (1954) reviewed the subject and concluded that, although the available records show the period of feeding activity, they do not tell the whole story. In general, both biting and flight activities follow the diel cycle, but there seem to be many variations within the active period. For example, there is a second peak of flight in some species, in the early morning hours, with a lower biting rate—either because many of the individuals have fed the preceding evening or because their activity is reduced by the lower temperatures. Moreover, it is usual to find considerable irregularity in abundance and biting activity in a given species.

Little has been published specifically on the flying and biting times of *C. tarsalis*. Bellamy and Reeves (1952) found that females of this species entered CO_2 traps "throughout the night, but there was a peak activity at sundown and a lesser one at dawn."

We observed under normal summer field conditions that the early-evening peak of flight—with or without biting activity—occurs in direct response to reduced light intensity, too low to be recorded accurately on the commonly used photographic light meter, i.e., less than 5 foot-candles. On warm evenings, when the mosquito population is high, large numbers appear suddenly at the end of twilight—very nearly at 30 minutes after sundown on cloudless evenings, though sometimes this flight starts later and sometimes—if the air is not so clear—as much as 10 minutes earlier.

The time of peak captures in CO_2 traps is within two hours after sunset. This interval is variable. We have given timed data for evenings when flight activity dropped suddenly at 45, 60, and 82 minutes after sunset, and in the first two instances the flights declined while temperatures remained above 70° F. In the third instance the temperature was still 68° when the catch dropped. Another experiment (August 19, 1963) showed a longer period of peak flight in the warmer of two locations that were only 1 mile apart.

On the other hand, this mosquito is not completely inactive at any time during the night, at least at temperatures as low as 59° F. The predawn increase in flight activity (again influenced by light intensity) is much lower than the twilight peak, and it may not occur if temperatures are much below 65°.

Height of Flight

Glick and Noble (1961) caught *C. tarsalis* over central Texas at 500, 1,000, and 2,000 feet. Glick (1939) caught some species of mosquitoes as high as 3,000 feet over Illinois and Indiana and 5,000 feet over Louisiana. He made significant meteorological observations and correlated the numbers of insects caught at different elevations with the temperature, wind velocity, and convectional currents at those elevations. The numbers of mosquitoes in the upper air were very small, especially in proportion to the numbers of some other insects.

In Delaware, MacCreary (1941) compared the catches of both freshwater and salt-marsh mosquitoes in light traps near the ground with those at 80 and 103 feet. With the exception of one night, the traps at 4 and 5 feet contained 85 to 96 per cent of the total catch.

In Arkansas, near a rice field, Horsfall (1942) collected specimens of *Psorophora confinnis* in motor-driven revolving nets 4 and 8 feet above the ground, operated continuously for two months. He found about 77 per cent of the catch of females at the 4-foot height and 73 per cent of the catch of males at the 8-foot height.

Bellamy and Reeves (1952), in California, caught *C. tarsalis* in CO_2 traps from ground level up to 25 feet or higher, with some of the larger catches at 14 feet or higher. Meyers (1959) also studied *C. tarsalis* in agricultural areas in California. His light traps collected more specimens at 25 feet than at either 5.5 feet or 50 feet. There was no significant difference in the sexes caught at each level.

The Sacramento-Yolo County Mosquito Abatement District maintained a light trap at a height of 1,540 feet on a television tower[11] in the Sacramento River delta region, where the prevailing winds blow strongly from the Golden Gate and San Francisco Bay. Along with small numbers of other common insects, the trap captured 22 specimens of *C. tarsalis,* of unknown origin, in the three-month period from August 30 to November 27, 1962, indicating that this cosmopolitan mosquito can be carried by wind for many miles at a considerable height above its normal range.

We believe that this mosquito usually flies at heights between 5 feet and 50 feet, where birds, a preferred host, roost in trees at night. As a flight habit persists for countless generations, it is unlikely that the blood-seeking individuals would normally fly above the upper story of the biosphere. Horsfall (1942) was of the same opinion concerning the species that he studied.

Dispersal Beyond the Rice Area

Brookman (1950) believed that *C. tarsalis* had no seasonal migratory trend in the lower San Joaquin Valley. At least it maintains a relatively high population there throughout the year, as indicated by collections in chicken houses and other shelters (Bellamy and Reeves, 1963). Stuntz (1952), Mortenson (1953), and Loomis and Green (1955) observed local fall movements into winter shelters, either in the hills or along streambeds, in the great interior valleys of California. Abell (1959), operating light traps at 850 feet elevation near an intermittent stream east of Fresno, found specimens of *C. tarsalis* about twice as numerous between October 16 and November 11, 1958, two to three months after local breeding had ceased, as they were during the summer months.

In the Sacramento Valley the males usually die by early November, and only the females seek hibernation quarters. When the large rice acreage is drained and harvested in September, and probably also in response to decreasing peri-

[11] With the cooperation of Trans-Tower, Inc.

ods of daylight, great numbers of females of this species move into temporary resting sites. Our observations are that the majority do not appear interested in biting, though they may nibble. They are restless and move about from shelter to shelter during the fall. As the weather gets colder individual mosquitoes scatter widely, either in the valley or in the hills, and remain hidden most of the time—in brush piles, hollow trees, loose rocks, rodent burrows, and some artificial shelters. In residential areas they are to be found in wood piles, in garages, under porches, etc. Farm buildings offer many places for overwintering, and many specimens are found there even though they prefer natural shelters. Probably many fail to survive, and others may be blown too far away to be traced. Those that survive hibernation become restless again in early spring.

From our limited collections over two winters and from our overall study of the habits of this species—supplemented by questioning the inhabitants in many hilly regions—we believe that there is a definite fall movement to the hills west of the Sacramento Valley, which have innumerable natural shelters and appear to be an important overwintering area. We found consistently higher winter populations in the hills on the west side than on the east—due probably to two factors: (1) The major rice acreage is on the west side of the river while orchard crops are dominant on the east. (2) The prevailing winds tend to push mosquitoes in this northwesterly direction from the rice fields.

On the west side *C. tarsalis* is sometimes found in significant numbers up to 1,725 feet, the greatest elevation at which we made winter collections. On the east side the densely wooded areas of live oak, willow thickets, and toyon, with heavy undergrowth, provide many hibernating sites at low elevations. These filter out the fall-migrating mosquitoes in most areas so that few of them are carried above 400 feet. However, we have collected this mosquito in hibernation in the Sierra as high as 3,539 feet. The site, in a barn near Lake Alta, was isolated completely by solid pine forests. Where specimens are collected at relatively high elevations in the Sierra they usually represent small populations breeding locally. There are some farm ponds in the foothills, as well as natural and man-made lakes.

We have no data on the spring flight habits of the overwintering population, but the winds usually would be against their return to the valley. Presumably *C. tarsalis* remains in the hills and starts breeding there in the spring. The species adapts itself readily to many of the different local conditions it encounters. However, the populations do not increase, because most of the streambed pools dry up in early summer. In any case, there are always sufficient numbers of mosquitoes overwintering in the valley to "seed" the rice area for the following season.

Summer Dispersal

Since this paper was submitted, Dow, Reeves, and Bellamy (1965) have published a report of experimental work in the San Joaquin Valley, where they found "widespread and continuous dispersal of female *C. tarsalis* throughout this region in the summer."

Patterns. The rice fields are the major source of mosquito populations in the Sacramento Valley. Most of them are near the Sacramento River, but their locations are scattered and some isolated fields of rice are planted among other crops. Usually, therefore, it was impossible to determine the origin of mosquitoes caught in open, rolling country, often subject to variable winds.

Both the terrain and the ground cover affect the flight pattern and the distribution of *C. tarsalis*. Stream banks, small hills, trees, and buildings cause updrafts, affecting air drainage, and influence the speed and direction of winds near the ground. Moreover, small towns and wooded areas are apt to disrupt a generally uniform dispersal of mosquitoes. In cities of 10 to 15 thousand population or more (e.g., Woodland) the highest mosquito catches are taken at the outskirts, but in small towns (e.g., Knights Landing) and in rural communities under 1,500 population (e.g., Yolo) large numbers of mosquitoes from nearby breeding areas scatter through the town nearly every evening.

Specific daytime resting sites of *C. tarsalis* are difficult to find because individuals do not cluster but rest singly—in weeds, tules, brush piles, etc., or under loose rocks, or on the soil itself. They are found in a daytime microenvironment with high humidity, low light intensity, and little or no air movement. They select the undersides of leaves, and stems with gray or dark-colored bark. If no suitable aboveground cover is available, both sexes may hide in the cool, deep cracks in the heavy soils of uncultivated or nonirrigated fields. We have observed many of them emerging from such cracks in the early evening.

From several thousand trappings over our five summers of study, in all the types of terrain in the county, we summarize our general observations on *C. tarsalis* and our conclusions from experimental data as follows:

1. Extensive movement takes place throughout the area on a typical summer evening.

2. The highest catches—obtained in 1961 and 1962, with 2,000 or more per trap—were made consistently in or near rice fields. Usually, but not always, progressively decreasing numbers were caught at increasing distances from a breeding source, especially in the upwind direction.

3. The smallest numbers were caught in large, barren fields, dry pastures, dry gulleys, and open, rolling country distant from breeding areas. However, in July and August, the situation would be extremely unusual if a CO_2 trap anywhere in the lower valley failed to catch any individuals of this species.

4. Individuals may move both up and down a canyon or streambed in the course of a single evening, in response to shifting wind directions.

5. *C. tarsalis* in this area drifting across open country tends definitely to seek the lee side of trees, levees, or buildings, where individuals stop for rest and where CO_2 traps make the best catches. Relatively large numbers in flight are usually caught also at points where a ditch, a stream, or even a road changes direction.

6. The majority of blood-seeking individuals fly at a low level, near the ground or 5 to 50 feet above it, with larger numbers at the lower levels.

Distance. It is impossible to know, in many instances, whether or not our recapture records represent either normal or maximum dispersal distances. Only a few miles from the release site the radial dispersal of the mosquitoes becomes so great that the odds against recapture are extremely high. On the other hand, the individual recaptured 15.75 miles from the release site might have traveled still farther that night and the next night if it had not been trapped. However, it is highly unlikely that it would have been recaptured at the greater distance.

In recapture data we can, of course, give only the airline direction and distance from release site to trap, because we have no knowledge of the indirect routes probably taken by many individuals. Recaptures on Night 0 are most significant, because the point of departure is known and we have records of the direction and velocity of the wind at the time and place of the release in addition to the continuous records at our field weather station. In the case of specimens recaptured on later nights, any of the innumerable daytime resting sites could have served as the starting point for the evening's flight.

Effective numbers of *C. tarsalis* disperse 2 and 3 miles downwind in one evening, and significant numbers can travel 7 miles or more in two evenings, with the aid of the wind. There are two record distances for recaptures in the entire series of experiments: 5 miles downwind on Night 0 (August 14, 1962) and 15.75 miles downwind on Night 2 (release of July 22, 1963). We believe it is realistic to estimate the likely dispersal distance of individuals in the Sacramento Valley at 20 to 25 miles. These mosquitoes travel with the wind so readily that without doubt all locally controlled areas are reinfested repeatedly during the summer.

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